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1977

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JUNE 1979

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7701

DISTRIBUTION, SIZE, AND ABUNDANCE OF MICROCOPEPODS IN THE CALIFORNIA CURRENT SYSTEM AND THEIR POSSIBLE INFLUENCE ON SURVIVAL OF MARINE TELEOST LARVAE[1]

DAVID K. ARTHUR[2]

ABSTRACT

The California Current system can be divided into onshore and offshore faunal zones by a copepod indicator species, *Mecynocera clausii*. Near the outer edge of the onshore zone copepod nauplii densities were higher than usual. There were about 3 times as many microcopepodids and 12 times as many nauplii on the average throughout the onshore as in the offshore zone. Feeding habits of larvae of sardines, anchovies, and jack mackerel may be adapted to the usual naupliar and copepodid concentrations of the zone in which they were spawned. The usual concentration of 56-μm and wider nauplii in the onshore zone was about 3/liter with 17 liter the highest observed which indicates that for nauplii of all sizes there were usually about 36 liter and with the highest density of 195/liter. These concentrations are lower than has usually been reported to be required for rearing larval fish in laboratories. Numbers of nauplii decreased exponentially with increasing size but a naupliar biomass maximum was found to occur at about the 70 μm width. Nauplii of this size are ingested at first feeding by Pacific sardine, northern anchovy, and jack mackerel larvae. It is suggested that larval feeding habits of these fish have evolved to utilize this important food resource at their first feeding.

Copepods form the bulk of most zooplankton hauls from the sea and are important because they are the main convertors of phytoplankton into food suitable for higher organisms (Marshall 1973). Copepods are especially important as food for planktonic larvae of pelagic marine teleosts. Food of the larvae of commercially important marine fishes has been widely reported as being primarily eggs, nauplii, and copepodid stages of small copepods. Yokota et al. (1961) found that food occurring in the feeding larvae of all the 57 species taken in their primarily coastal samples was almost entirely small copepods, especially nauplii. Duka and Gordina (1973) investigated the food of larvae of 26 species of teleosts from the Mediterranean and adjacent areas of the Atlantic and reported that copepod nauplii composed 90% of all items eaten by small larvae (2.3 to 5.0 mm). Stomach content analyses of fish larvae are also corroborated by population dynamic studies of plankton organisms. Fish (1936) noted that in the Gulf of Maine a small copepod, genus *Pseudocalanus*, suffers a much higher predation rate during the naupliar stages than does *Calanus finmarchicus* whose eggs (140 μm wide) and nauplii are too large to be ingested by many fish larvae.

When it became apparent that the population of Pacific sardine, *Sardinops sagax*, was in serious decline, a research program [later to become known as CalCOFI (California Cooperative Oceanic Fisheries Investigations)] was initiated in 1949 to investigate the ecology of this important fish. One part of this investigation was a study of the food and food resources of sardine larvae and consisted of two main objectives: 1) determine what the larvae eat, and 2) to study the abundance and distribution of these food items. The ultimate purpose was to determine if feeding conditions, especially for the first feeding larvae, could be a contributing factor to the sardine's decline, as was proposed by Hjort (1914) to explain poor year class survival of fishes in general.

The identifiable food of first feeding sardine larvae was primarily copepod nauplii ranging from 25 to 80 μm but mostly about 70 μm wide (Arthur 1976). Nauplii of this size are produced only by small species of copepods, roughly less than 1.5 mm long. The assemblage of these small copepods is composed of many species. Several genera have often been recorded as being abun-

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[1] Based on a portion of a dissertation submitted in partial satisfaction of the requirements for the Ph.D. degree at the University of California, Scripps Institution of Oceanography.

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Manuscript accepted January 1977
FISHERY BULLETIN: VOL. 75, NO. 3, 1977

dant in the plankton as well as in the intestinal contents of larval fishes. Among these are the cyclopoid genus *Oithona,* (especially *O. similis*), and the calanoid genera *Pseudocalanus* and *Paracalanus. Oithona similis,* whose first stage nauplius is 70 μm wide (Oberg 1906) and can, therefore, be ingested by sardine larvae, composed over 50% of the cyclopoid fauna in 37 of the 42 samples off Oregon through Baja California examined by Olson (1949). Because of the large number of species, many of whose developmental stages had not been described, no attempt was made in this study to identify eggs, nauplii, and copepodid stages to species.

This report deals with size, abundance, and distribution of naupliar and copepodid stages of copepods captured with relatively fine meshed plankton samplers in and near the California Current. These small species of copepods will be referred to as microcopepods, and all postnaupliar stages, including adults, as copepodids. The term nauplii will include true nauplii and metanauplii.

SAMPLING METHODS

The need for a study of the small crustacean plankton was anticipated early in the CalCOFI program. The 1-m net with its relatively coarse mesh (505 μm) was considered adequate for sampling sardine eggs and large copepods and euphausiids, but most small copepods and nauplii pass through this size mesh. Starting in May 1949, a Clarke–Bumpus sampler (Clarke and Bumpus 1940) equipped with a #8 mesh bolting silk net, (203 μm in unused condition) was used routinely at stations in the central and upper southern California areas. It was towed obliquely from a depth of 70 m, filtering about 5 m^3 of water.

The Clarke–Bumpus sampler was abandoned after March 1950 in favor of the "high-speed sampler" (California Academy of Sciences et al. 1950) which was modified by having a mouth diameter of 7.6 cm, the same as the main fuselage of this device, rather than being tapered to a narrower opening as in the original high-speed sampler. It was equipped with a 143-μm wire filter and was towed on the same wire as the meter net and was used because the record it made of depth versus volume of water filtered could be used to analyze the meter net track as well as its own. This modified version was called the "microplankton sampler." It was towed obliquely from a depth of 70 m during March 1950–September 1950 and from 130 m on cruises from November 1950 to July 1952.

After a study had been made of the food ingested by ocean-caught sardine larvae, it became obvious that very small copepod nauplii are critical in the ecology of these larvae. Therefore, after August 1951 a plankton sampler of much finer mesh was used. This sampler was essentially a medium Epstein net (Sverdrup et al. 1942:379) with a mouth opening 17.5 cm in diameter, connected by a canvas collar to a filtering cone constructed of #20 bolting silk (76 μm in unused condition). This sampler was hauled vertically from a depth of 50 m and was called the "truncated net."

These three plankton samplers were used between May 1949 and September 1954. Pertinent statistics are compared as follows:

Sampler	*Mouth diameter (cm)*	*Mesh aperture size (μm)*		*No. of samples*
		New	*Used*	
Clarke–Bumpus	12.5	203	120	185
Microplankton	7.6	143	143	612
Truncated net	17.5	76	56	239
				1.036

Because of expansion when wet, and the unraveling of threads when used, the aperture size of used wet silk nets is considerably smaller than new dry ones. The above "used" values were obtained by measuring aperture sizes, when submerged in water in the laboratory, of nets being used in the collections. Even with the smallest aperture size used (56 μm) many nauplii and copepodids must have escaped. Beers and Stewart (1967) reported that a significant quantity of copepods pass through a 35-μm mesh. Most food particles of sardine, anchovy, and jack mackerel larvae, however, are wider than 56 μm (Arthur 1976.)

COUNTING METHOD

The plankton samples were examined in a plastic chamber measuring 60 mm by 70 mm, the floor of which was lined every 5 mm to form a grid. Its total fluid capacity is approximately 50 ml with a water depth of about 12 mm. In practice, the fluid volume in the chamber measured less than half of this. If the amount of material in the sample was not too great, the entire sample was counted. Most samples taken with the Clarke-Bumpus and truncated nets contained so much material that subsampling was necessary. This was accomplished by first measuring the total fluid volume of the sample, then stirring it vigorously to disperse the material, then drawing off a convenient amount for examination, and finally measuring the remainder in order to determine what percentage the subsample was of the original sample.

FAUNAL AREAS IN THE CALCOFI SECTOR

Although the primary purpose of the microplankton program was a quantitative appraisal of the microcopepod fauna, a few prominent copepod species were routinely recorded. One of these, *Mecynocera clausii*, proved useful as an indicator organism allowing the CalCOFI sector to be roughly divided into two plankton faunal areas, onshore and offshore.

Mecynocera is a monotypic genus. It can readily be distinguished from other copepods by its exceptionally long first antennae (Mori 1964). Its small size (about 1 mm) places it within the microcopepod range. These attributes make it convenient and useful as an indicator of conditions affecting the microcopepod fauna. *Mecynocera clausii* has been reported near the surface throughout tropical areas of the oceans, as well as in temperate areas such as the Mediterranean. In the CalCOFI area its presence may be considered as indicating the more tropical offshore and southern waters.

A typical distribution of *M. clausii* off southern California and off northern and central Baja California is illustrated by data for February 1951 (Figure 1). *Mecynocera* is characteristic of offshore water whereas the occurrence of plutei of benthic echinoderms may indicate coastal water. The two boundaries tend to interdigitate, which must imply alternating tongues of warm offshore water penetrating toward the coast and jets of cold onshore water moving out to sea. The 15°C isotherm supports this interpretation.

Submergence of the water of the California Current under the offshore subtropical water may be indicated at stations where *Mecynocera* and plutei were taken together. This would result if the net in its 130-m deep track caught *Mecynocera* near the surface and plutei at some depth where the submerging water had carried them.

The shoreward boundary of *Mecynocera*, as determined by the various cruises, is presented in Figure 2. In general, the average boundary is found about 400 km offshore in the San Francisco area and inclines toward the coast farther south. In the northern Baja California area it may impinge upon the shoreline, but it becomes erratic in the turbulent Punta Eugenia area.

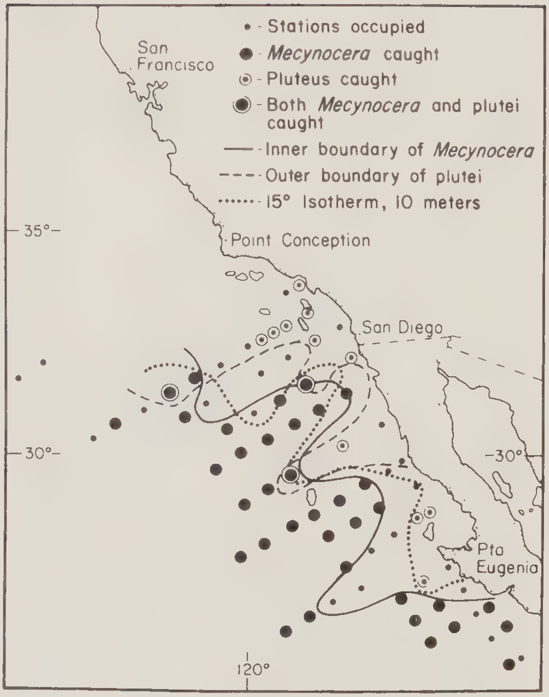
• - Stations occupied
● - *Mecynocera* caught
⊙ - Pluteus caught
◉ - Both *Mecynocera* and plutei caught
—— - Inner boundary of *Mecynocera*
- - - - Outer boundary of plutei
······ 15° Isotherm, 10 meters
San Francisco
Point Conception
San Diego
Pta Eugenia
35°
30°
30°
120°

FIGURE 1.—Distribution of *Mecynocera clausii* and pluteus larvae during CalCOFI cruise for February 1951 off California and Baja California.

ZONE OF COPEPOD NAUPLII MAXIMUM

For a given cruise, if each line is examined and the station which contained the greatest concentration of nauplii is circled and the circled stations for the various lines are connected, one obtains a line of maximum copepod nauplii concentrations. Figure 3 presents a typical distribution of copepod nauplii and their maximum zone in the Channel Island area. Two stations have been circled for the line extending offshore from San Diego. It is common to find a high local concentration at stations near the coast and a second high offshore particularly in the area north of Point Conception. Had the station pattern extended closer to the beach, higher concentrations of nauplii probably would have been encountered there. During a 5-mo

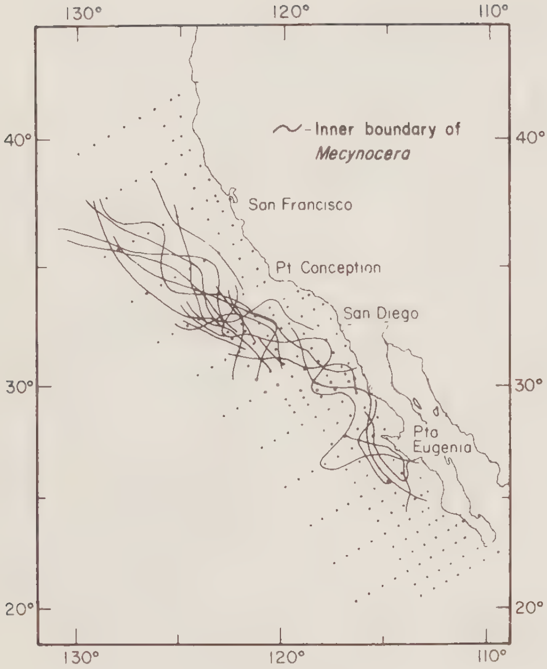
130°
120°
110°
40°
30°
20°
-Inner boundary of *Mecynocera*
San Francisco
Pt Conception
San Diego
Pta Eugenia

FIGURE 2.—Inner boundary of *Mecynocera* for individual CalCOFI cruises from June 1949 to July 1951 off California and Baja California.

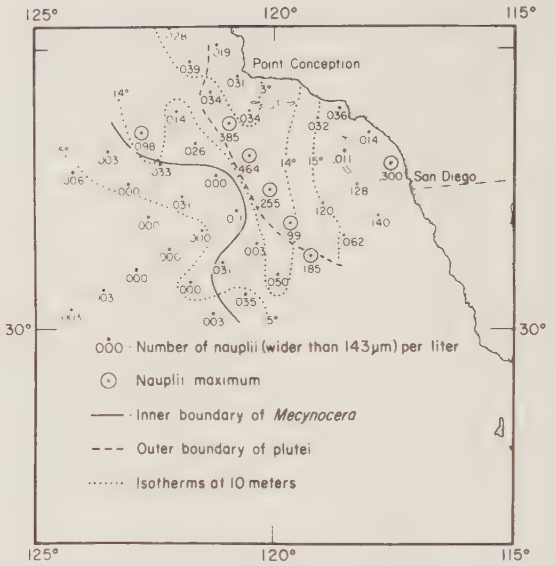
125°
120°
115°
30°
Point Conception
San Diego
14°
15°
5°
3°
385
464
255
99
185
300
000 · Number of nauplii (wider than 143μm) per liter
Nauplii maximum
Inner boundary of *Mecynocera*
Outer boundary of plutei
Isotherms at 10 meters

FIGURE 3.—Distribution of copepod nauplii (wider than 143 μm) and their relation to some other biological and physical variables during June 1950.

study of plankton off La Jolla, Beers and Stewart (1970), using 35-μm mesh nets, found that for the three stations located 1.4, 4.6, and 12.1 km from shore, naupliar densities averaged 63/liter, 33/liter, and 26/liter, respectively.

The zone of maximum nauplii seems to be associated with the *Mecynocera* boundary, which is also indicated in Figure 3. The station of maximum nauplii for a line usually occurs one to three stations onshore of this boundary.

As may be seen in Figure 3, there appears to be an association between the zone of maximum nauplii and the tongue of relatively cold water (13° and 14° isotherms) extending south of Point Conception. This cold tongue probably is nutrient rich water upwelled north of Point Conception. Shoreward from this zone lies the counterclockwise gyre of the Southern California Bight, extending from Point Conception to northern Baja California. Allen (1939) stated that his most offshore station, located 120 km from the coast, which is in the general vicinity of the nauplii maximum, was consistently the richest station for microcrustacea. Berner (1959) noted that stations where he found anchovy larvae to be feeding were in the area of the copepod nauplii maximum as described by Arthur (1956).

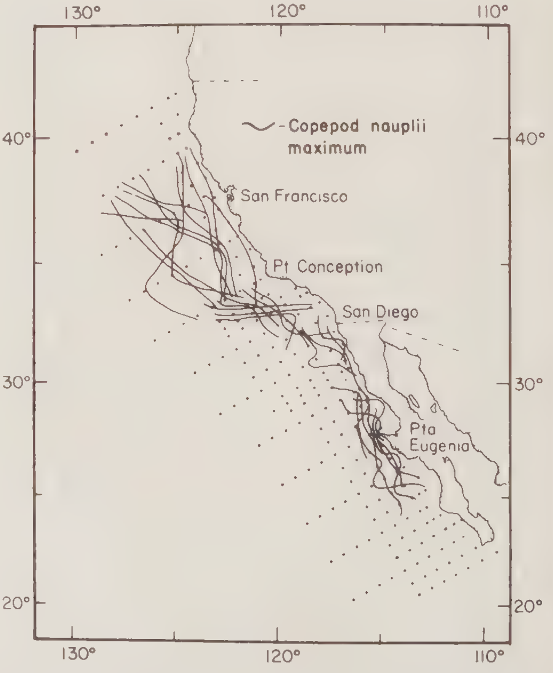
130°
120°
110°
40°
30°
20°
-Copepod nauplii maximum
San Francisco
Pt Conception
San Diego
Pta Eugenia

FIGURE 4.—Copepod nauplii maxima for individual CalCOFI cruises from June 1949 to July 1951.

In the San Francisco area, where two maxima are commonly found, the outer one is usually about 115 to 400 km offshore (Figure 4). The maximum zone is consistently found seaward from the Channel Islands, about 100 to 320 km off the mainland shore. Occasionally nauplii-rich stations are found inside the islands. The average nauplii maximum approaches the coast south of San Diego, and is adjacent to the shoreline in northern Baja California, probably a result of upwelling along the coast. From Punta Eugenia south, this zone becomes irregular, as does the *Mecynocera* boundary.

QUANTITATIVE DISTRIBUTION OF MICROCOPEPODIDS AND NAUPLII IN THE CALCOFI AREA

On examining the values obtained in this program, it is apparent that there are very wide ranges in densities. Values for microcopepodids range from 0.003 to 7.886/liter. Nauplii were sampled in numbers ranging from 0 to 17.280/liter. Frequency distributions are highly skewed toward the lower densities. To overcome this problem, the data are presented as logarithms to normalize the frequency distributions.

The method used for comparing data is the ogive, or cumulative frequency curve. The ogive is useful to depict what percentage of the samples from an area contains any particular concentration of copepodids or their nauplii. Furthermore, in considering concentrations of any two areas, the value of the 50 percentile concentrations can be quickly read off and compared. The 50 percentile value in this particular type of distribution lies very near the mode and so may be considered to closely represent the most common value of concentration for a given area.

Ogives for nauplii and microcopepodids as sampled by all Clarke–Bumpus and all microplankton samples in both the onshore zone and offshore zone are presented in Figure 5. Because of the large mesh size of the nets used, most nauplii escaped which resulted in more copepodids than nauplii being caught. The truncated net (56-μm mesh) caught more nauplii than copepodids. Very few samples were taken in the offshore zone with the truncated net and so it cannot be compared with the other two samplers in this manner. Differences in the ratios of onshore zone to offshore zone for the 50 percentile values are as follows:

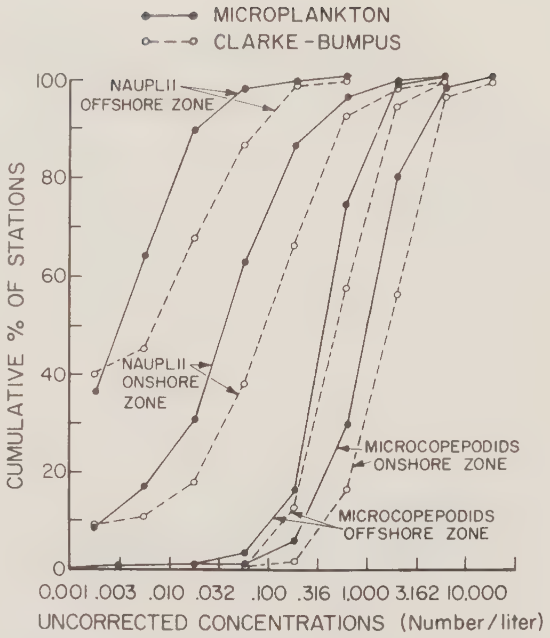

FIGURE 5.—Ogives for abundance of nauplii and microcopepodids in offshore and onshore zones as sampled with the Clarke–Bumpus (120-μm mesh) and microplankton samplers (143-μm mesh).

Sampler	*Microcopepodids*	*Nauplii*
Clarke–Bumpus	3.17:1	12.58:1
Microplankton	2.57:1	11.22:1

There are about two and one-half to three times as many copepodids in the onshore zone as there are in the offshore zone. There are, however, about 12 times as many nauplii in the former as in the latter. There are about four times as many nauplii per copepodid in the onshore zone as in the offshore zone. This is probably a result of the increased fecundity of copepods living in the richer phytoplankton owing to upwelling in the onshore zone.

CORRECTING FOR CALIBRATION ERRORS AND ESCAPEMENT

The ogive was useful to correct errors of the various samplers used in this survey. Figure 6 presents the ogives obtained for microcopepodids by all samples taken in the onshore zone with the three different samplers. Of the three samplers, the Clarke–Bumpus was the most accurately calibrated for volume and so the other two samplers were corrected to it. Such a correction can be made

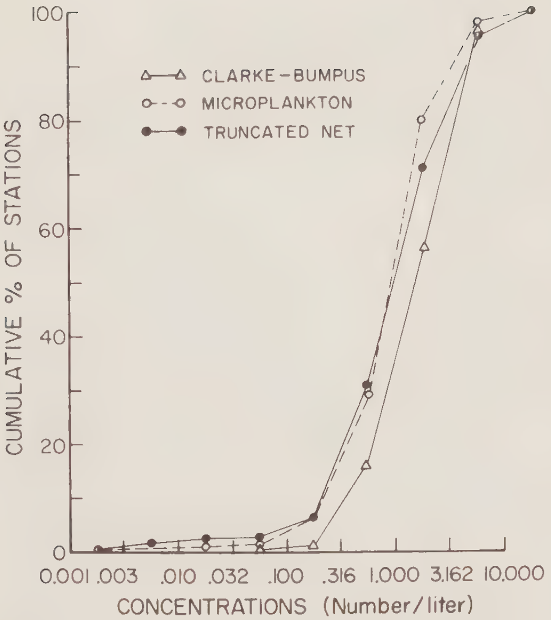

FIGURE 6.—Ogives for abundance of microcopepodids in the onshore zone as sampled by the three samplers.

by measuring their 50 percentile differences and adding this value to all the points along their respective curves. This correction assumes that all net meshes used retained copepodids in equal percentages. This is not entirely correct as Beers and Stewart (1967) reported that some copepodids can escape even a 35-μm mesh.

Having corrected the volume errors of the three devices (or, at least, made them comparable in value), we can now roughly correct for the amount of escapement by nauplii through the three different mesh sizes. Figure 7 presents ogives for nauplii in the onshore zone as sampled by the three devices, the numbers of which have been corrected for volume strained by values obtained by the 50 percentile differences in Figure 6. These ogives are based upon the same amount of water filtered, thus their differences are due to differential escapement of nauplii. By comparing the 50 percentile values in Figure 7, the following approximation of the size distribution of the naupliar population in the onshore zone is obtained:

Sampler	*Mesh opening (μm)*	*Usual number retained/liter*
Truncated net	56	2.884
Clarke–Bumpus	120	0.095
Microplankton	143	0.058

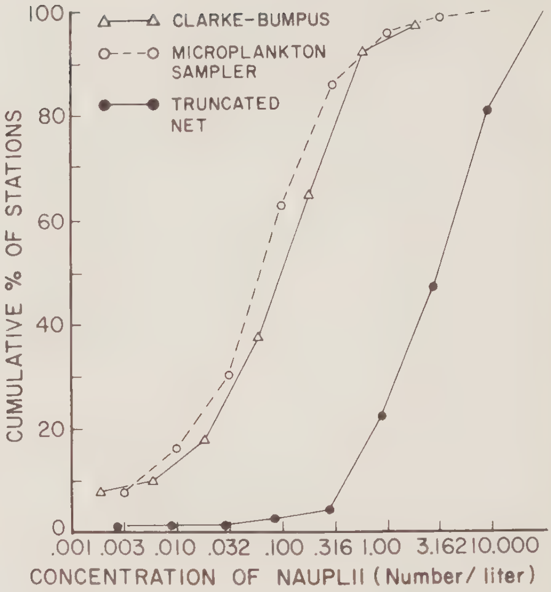

FIGURE 7.—Ogives for nauplii of all sizes retained by each of the three samplers in the onshore zone corrected for volume filtered.

A plankton net hauled from some depth to the surface may pass through a wide range of plankton concentrations but its catch will represent only the average of these conditions and will not reveal rich but thin strata that might exist. The above concentrations, therefore, probably underestimate somewhat the highest concentrations found in the usual water column.

When the ogives for the three samplers are corrected to the Clarke–Bumpus for volume and to the truncated net for escapement, by their 50 percentile differences (Figure 8), they are similar over the mid-60% of their ranges. It is interesting that the three curves for nauplii are so similar when it is considered that two of them represent, primarily, the small percentage contributed by larger nauplii. This implies that the various sizes of nauplii have essentially the same type of distribution and with the same degree of patchiness.

The slope of an ogive is determined by the degree of dispersion within the samples. If the distribution of an organism is so homogeneous that all the observations should fall in one interval, then the resultant ogive would be a vertical line. With wider ranges of densities the ogive will slope less abruptly. By comparing slopes of the two sets of ogives in Figure 8, it can be seen that the copepodid stages are more uniformly distributed than are nauplii.

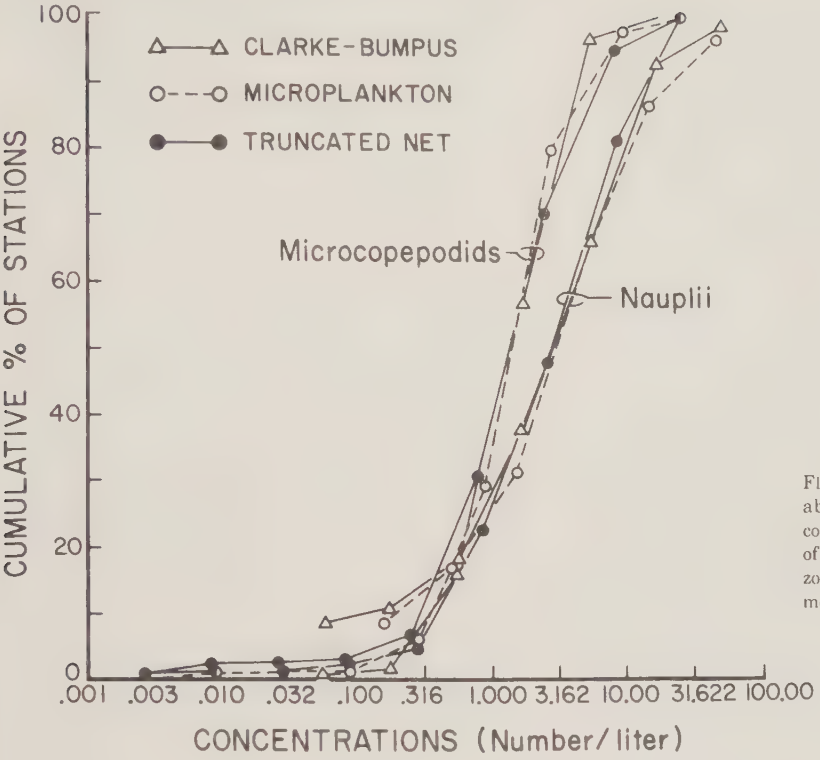

FIGURE 8.—Comparison of ogives for abundance of nauplii and microcopepodids for all sizes retained by each of the three samplers in the onshore zone corrected for volume and escapement.

DISCUSSION

Microcopepod Size and Feeding Habits of Three Larval Fishes

Feeding habits of larvae of Pacific sardine, *Sardinops sagax*; northern anchovy, *Engraulis mordax*; and jack mackerel, *Trachurus symmetricus*, as reported by Arthur (1976), may have been associated with spawning distribution of the adult fish as well as with the distribution of microcopepods and nauplii during the years of this program. Jack mackerel spawned mainly in the offshore zone, as can be determined by comparing the *Mecynocera* boundary with the distribution of jack mackerel larvae (Anonymous 1953:36). Jack mackerel larvae first start to feed when 3.0 mm long and ingest mostly 60- to 70-μm wide (total range 50 to 200 μm) copepod nauplii. However, when they have grown to 3.5 mm their food is primarily about 125-μm wide copepodid stages of small copepod species and when 9.0 mm long they eat 250- to 450-μm wide copepodids of larger species. The quick change from nauplii to copepodids, which is facilitated by their relatively large mouths, may be related to the low nauplii/copepodid ratio of the offshore zone.

Most anchovy larvae were caught inside the *Mecynocera* boundary (Anonymous 1953:34). The more omnivorous 3.0-mm long first feeding anchovy larvae select food from the 25 to 100 μm range with little preference for any size within this range. Food size increases to 125 μm when larvae are about 4.0 mm after which, though there is some increase, food size does not increase isometrically with the increase in length of larvae. This curious slow increase in food size appears to be common to early larval stages of the genus *Engraulis*, as can be observed in food-size/larval-length graphs for Japanese anchovy, *E. japonica* (Yokota et al. 1961), Argentine anchovy, *E. anchoita* (Ciechomski 1967), Peruvian anchovy, *E. ringens* (Rojas de Mendiola 1974), and can be calculated for northern anchovy, *E. mordax*, from data presented by Berner (1959) and Arthur (1976). This lack of selecting for the largest ingestible food size may be related to the high nauplii/copepodid ratio of the inshore zone and may also account for the importance of copepod eggs in the diets of anchovy larvae as reported by the above authors except Yokota et al. (1961).

Sardines spawn near the *Mecynocera* boundary, inshore of the jack mackerel and mostly offshore of anchovy (Anonymous 1953:22), but, also, more southerly of the other two. Sardine larvae combine some feeding characteristics of jack mackerel and anchovy larvae. Food particle size of sardine larvae increases isometrically with length of larvae as in jack mackerel but is smaller for unit larval length and is composed more of copepod eggs and nauplii as in anchovy larvae.

Microcopepod Densities Influence Larval Fish Survival

Other investigations in the CalCOFI area, and in similar latitudes in Japanese waters, helped to approximate the biomass spectrum of the naupliar population. Beers and Stewart (1967) estimated numbers of various microzooplankton at five locations across the California Current. Samples were taken by pumping water through several sizes of filters from depths ranging from the surface to 105 m. Their values for copepod nauplii, averaged and integrated, are compared with the values reported herein as follows:

Mesh size	*Nauplii/ liter*	*Logrithm*	*Source*
Total no., all sizes	22.078	1.3440	Beers and Stewart
Retained by 35 μm	3.878	0.5886	Beers and Stewart
Retained by 56 μm	2.884	0.4600	This report
Retained by 103 μm	0.198	−0.7033	Beers and Stewart
Retained by 120 μm	0.095	−1.0223	This report
Retained by 143 μm	0.058	−1.2366	This report

Logarithms of the above, plotted in Figure 9, are highly correlated with mesh size for the two individual sets of data as well as when they are combined. The line in Figure 9 is a least square fit to all data points combined and is expressed as:

$$N = -0.0188w + 1.3370 \quad \text{(intercept at size 0)} \qquad (1)$$

where N is concentration of nauplii (number per liter) and w is mesh aperture size. The correlation coefficient, r, is 0.9931 and the coefficient of determination, r^2, implies that 98.62% of the variation of naupliar concentrations can be explained by mesh size alone.

Least square fits for the two individual sets of data are as follows:

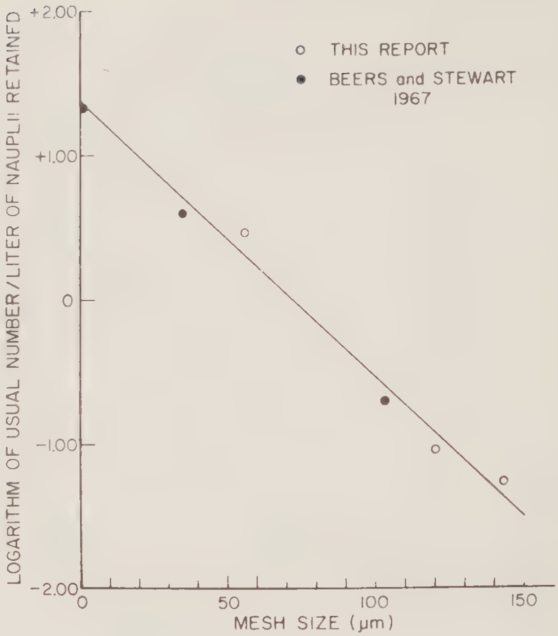

FIGURE 9.—Logarithms of the usual densities of various sizes of nauplii in relation to mesh size. The line is a least square fit to all data points combined from the equation $N = -0.0188w + 1.3370$.

Beers and Stewart

$$N = -0.01976w + 1.31857 \qquad (2)$$
$$r = 0.9994,\ r^2 = 0.9988.$$

This report

$$N = -0.02029w + 1.5577 \qquad (3)$$
$$r = 0.9900,\ r^2 = 0.9801.$$

The microcopepod assemblage in onshore water off the southern California–northern Baja California coast is strikingly similar to that in coastal waters at the same latitudes on the other side of the Pacific. Yokota et al. (1961) measured widths and lengths of 8,839 copepod nauplii and 1,389 copepodids from 666 samples captured in 1-liter containers from an area off the southeast coast of Kyushu over a 2-yr period. Average widths and lengths of nauplii were 67.7 and 156.1 μm, respectively, with a length to width ratio of 2.306. Assuming a cylindrical form, the average Kyushu nauplius has a volume of about 562,000 μm^3 which differs by only about 10% from the 510,000 μm^3 volume of the average La Jolla nauplius (Beers and Stewart 1970). Concentrations ranged from 0 to 524 nauplii/liter (only two samples were greater than 100/liter) with an average of 13.27/liter. Size distribution as calculated from the data of Yokota et al. (1961) is:

Width of nauplii	*Average number/liter*
All sizes	13.27
>50 μm	3.87
>100 μm	0.53
>150 μm	0.10
>200 μm	0.05

In comparing the Kyushu to the California area it appears that there are fewer very small nauplii but about twice as many larger nauplii. These differences may result from the Kyushu samples being taken at the surface whereas the California samples were collected at varying depths.

Usual densities of total nauplii and copepodids of all sizes calculated from the several investigations discussed herein are as follows:

Nauplii/ liter	*Copepodids/ liter*	*Source*
36.12	1.41	This report, Equation (3)
13.27	2.10	Averaged from Yokota et al. 1961
22.08	36.35	Averaged from Beers and Stewart 1967
34.33	4.17	Averaged from Beers and Stewart 1970

The calculated number of nauplii of all sizes from this report appears to be somewhat high which may result from being derived by extrapolating from Equation (3). The average number of copepodids found by Beers and Stewart (1967) appeared to be much higher than the other investigations and may be a result of sampling an unusually rich but short-lived condition (all samples were taken during a 7-day period). Numbers of nauplii and copepodids of Beers and Stewart (1970) should be somewhat higher than the average for coastal areas because they were taken very close to the beach. In general, the usual densities in onshore areas at these latitudes (30°–35°N) is about 1.5 to 4 copepodids/liter and about 13 to 30 nauplii/liter. These densities are similar to those found by Allen (1939) who, while studying phytoplankton off California by trapping 5-liter samples, found that the combined densities of nauplii and copepodids ranged from 10 to 30/liter. Copepod nauplii average about 20–30/liter in Japanese coastal waters and 10 or less/liter in the warm offshore Kuroshio (Honjo et al.[3,4]).

These densities are considerably lower than those usually reported to be required to support growth of marine teleost larvae in the laboratory as is illustrated by a few examples. O'Connell and Raymond (1970) found poor survival of anchovy larvae in densities of nauplii and copepodids of less than 4,000/liter. Hunter (in press) used 100,000 *Gymnodinum*/liter combined with 8,000 to 115,000 rotifers/liter to grow early anchovy larvae. Houde (1975) found best survival of larval sea bream, *Archosargus rhomboidalis*, was on 50- to 100-μm wide nauplii and copepodids in densities of 1,500–3,000/liter, but 10% survived at 100/liter at low larval stock densities. In coastal and offshore areas even the highest densities of nauplii reported do not equal those used in most laboratory rearing experiments. The highest concentration of larger than 56-μm nauplii I encountered was 17.28/liter which indicates that, calculating from Equation (1), for nauplii of all sizes there were about 195/liter. Highest concentrations reported by others are 524/liter (Yokota et al. 1961), 180/liter (Beers and Stewart 1970), and 134/liter (Allen 1939).

Gallagher and Burdick (1970) calculated that the mean distance $\bar{R}$, between a particle and its nearest neighbor in a random three-dimensional array can be computed from $\bar{R} = 0.553960\rho^{-1/3}$, where ρ is their mean density in space. At concentrations of 25 nauplii/liter the distance from the mouth of a fish larva to the nearest nauplius is on the average about 18.9 mm, whereas at 200 nauplii/liter this distance is 9.5 mm.

Concentrations approaching laboratory requirements are encountered in localized conditions, i.e., Schnack (1974) caught nauplii with a 55-μm net in numbers up to 917/liter in a shallow fjord off the western Baltic. Lasker (1975) found the dinoflagellate, *Gymnodinum splendens*, in the ocean in high enough densities (20,000–40,000/liter) to support life of early laboratory-spawned anchovies. These densities were dependent on stable oceanic conditions which were quickly dispersed by a storm.

The reason for the disparity between the observed naupliar densities in the ocean and the

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[3] Honjo, K., T. Kidechi, and H. Suzuki. 1959. On the food distribution and survival of post larval iwashi-I-Distribution of food organisms, the food of the anchovy and ecologically related species along the southwestern Pacific coast of Honshu, Sept.–Nov. 1958. Reports on the major coastal fish investigations, and the investigations for forecasting of oceanographic conditions and fisheries (Preliminary Report), February 1959, 7 p. Engl. transl. by S. Hayashi.

[4] Honjo, K., T. Kitachi, and M. Kudo. 1957. Food of the postlarvae of iwashi. Reports of the major coastal fish investigations for 1956 (Preliminary Report) November 1957, 5 p. Engl. transl. by S. Hayashi.

densities required for larval survival in the laboratory may be that present microplankton sampling techniques do not detect small but dense aggregations of nauplii which, however, can be found by fish larvae. It, also, may be that present rearing techniques do not approximate oceanic conditions sufficiently to permit assaying of actual prey concentrations required to allow significant larval survival. Blaxter (1965) reported that the condition factor of herring larvae living in the ocean is worse than that of larvae which died presumably of starvation in the laboratory. This may attest to greater ability of larvae to survive poor rations in the usual oceanic environment than in the laboratory.

Maximum of Naupliar Biomass Spectrum

The abundance of copepod nauplii decreases exponentially with increasing size of individuals (Figure 9), whereas the volume of an individual nauplius increases exponentially with increasing size (roughly by the cube of width). When the naupliar size range is divided into 10-μm wide size classes and the average volume per nauplius is multiplied by numbers of individuals per class (calculated from the equation for combined data, Figure 9) it is seen that the naupliar biomass is at a maximum at about the 70 μm width (Figure 10) even though there are many more nauplii of smaller sizes.

Figure 10 includes, also, the food-particle size range at first feeding of larvae of Pacific sardine, northern anchovy, and jack mackerel (Arthur 1976). It is interesting to note that these ranges overlap at the 50- to 80-μm width range which brackets the naupliar biomass spectrum maximum. This suggests that larval feeding habits of these three fishes have evolved to take advantage of this important food resource at first feeding.

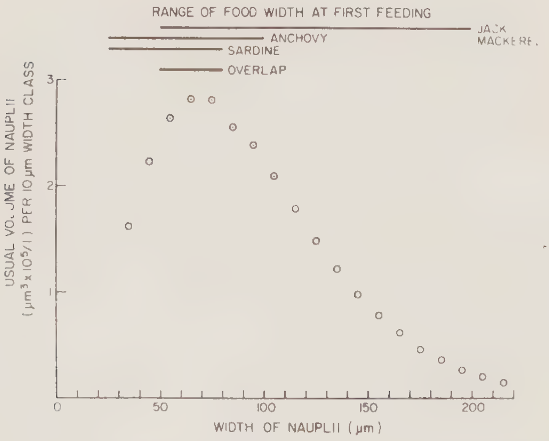

FIGURE 10.—Biomass spectrum of naupliar size range compared with food size at first feeding of the larvae of three fishes in the California Current system.

ACKNOWLEDGMENTS

I express my appreciation to Martin W. Johnson, Reuben Lasker, and Paul E. Smith for their helpful comments and criticisms during the preparation of the manuscript.

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CLIMATOLOGY OF UPWELLING RELATED PROCESSES OFF BAJA CALIFORNIA

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ABSTRACT

Marine surface data are used to describe large scale features of upwelling and certain related processes off the west coast of Baja California. The offshore-directed component of sea surface Ekman transport, computed from the wind stress distribution, is considered an index of coastal upwelling intensity. Upwelling appears to be strongest south of 30°N latitude, from March to June. Departures from randomness in the offshore Ekman transport signals include the annual and diurnal periodicities, an energetic irregular rhythm in the "event" frequency range (several day to several week periods), and two types of persistence. A short-term persistence appears to be related to the duration of synoptic scale atmospheric disturbances, while a much longer-term persistence may be related to a feedback mechanism between the upwelling and the overlying wind stress field.

The longshore current field is highly correlated seasonally with the upwelling cycle. Strong equatorward surface flow is indicated during the spring upwelling maximum; during the fall there is generally a poleward component of flow. Wind stress curl distributions indicate a tendency for the surface wind drift to be convergent (negative curl) in the offshore region. From Punta Baja to Punta Eugenia the convergent area extends to the coast. Areas of divergent surface drift (positive curl) extend several hundred kilometers off the coast north of Punta Baja and south of Punta Eugenia. From a "Sverdrup transport" point of view, this pattern is consistent with evidence of separate cyclonic gyral circulations north of Punta Baja and south of Punta Eugenia.

INTRODUCTION

Coastal upwelling is a highly fluctuating process which can have important effects on fishery resources. The role of upwelling in bringing nutrients into the surface layers where they are available for organic production is widely recognized. A related process that may enhance production is the dispersion of grazing organisms by the diverging surface waters, thereby reducing grazing pressure on the phytoplankton stock. In addition to these effects at the very base of the food web, upwelling can alter the temperature distribution, field of motion, stratification, and other characteristics of the physical environment, affecting marine organisms at various levels of their life processes.

At the Pacific Environmental Group we are developing descriptions of upwelling phenomena to aid fishery researchers in accounting for such effects. To be most useful these descriptions should have continuity over the broad space scales and long time scales involved in fishery work. In addition it is desirable that they be continually updated and hindcast over past periods for which knowledge of a fishery is available. Our approach, consequently, has been to avoid basing our work on dedicated observational programs but rather to try to construct a useful descriptive system from observatons routinely reported by ships at sea, weather stations, etc.

Our collocation with the U.S. Navy's Fleet Numerical Weather Central (FNWC) in Monterey, California, provides access to a broad data base including archived historical data, analyzed meteorological products, and real time reports. Several data sources have proven most fruitful. The National Climatic Center's file of marine surface observations has been useful in defining the climatological seasonal cycles. This file contains over 38 million individual ship reports, dating back into the nineteenth century. Similar real-time ship reports continue to be delivered via the international data networks. To describe variations from normal seasonal conditions we have used the analyzed products, notably the surface atmospheric pressure analysis, produced by FNWC. Finally, the U.S. Naval Oceanographic Office ship drift file, which is a compilation from ships' log books of differences between dead reckoning position and accurately detemined position, has been useful as an indication of the seasonal variability of the ocean surface flow field.

Our major focus is the upwelling region off western North America. However, since the data sources are global the methods developed should be applicable to other regions, depending on the density of available data. At this stage much of our work is qualitative. Our goal is to model quantitatively many of the processes which would be useful environmental inputs to fishery management systems for upwelling regions, and to define and develop practical indicator systems to make these inputs operational.

THE SEASONAL CYCLES

To define seasonal variations, long-term composite monthly distributions of various properties were assembled from ship reports contained in the National Climatic Center's file of marine surface observations (TDF-11). After preliminary gross error checks, similar to those described by Bakun, McLain, and Mayo (1974), climatological scalar properties were compiled by computing the arithmetic means of all available reports within a specified 1-degree square area and long-term (1850–1970) month. Similarly, resultant mean vector quantities have been computed as the arithmetic means by north and east components for all reports in the area. A mean value for any month and square is therefore formed from a data set that is independent of all other months and squares. No attempt has been made to smooth the fields, either by removing data which do not appear to fit the distributions or by applying objective smoothing procedures. The mean values were contoured by machine, and "bulls eyes" in the contours, even where they possibly reflect erroneous data, were left in the figures as indications of the general degree of consistency of the composite fields.

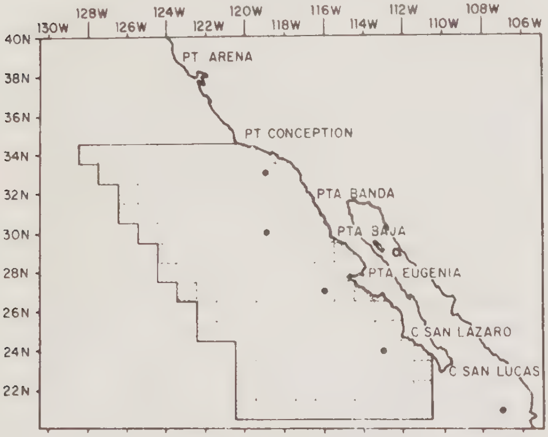


FIGURE 1. Chart of the Baja California region The grid of 1 degree squares is used for summaries of ship observations. Shading indicates nearshore and offshore lines of selected squares parallel to the coast and lines extending westward from the coast south of Punta Baja and Punta Eugenia used for displays of time-space sections. Large dots indicate 3 degree grid intersections used to compute time series properties.

Approximately 400,000 individual reports are available for the area defined by the grid off southern California and Baja California (Figure 1). The number of reports per 1-degree square per month varies from less than five (in May in the southwest section of the grid), to 3500 (in May off Los Angeles). The spatial distribution of observations is biased in that "ship of opportunity" reports are generally confined to coastwise shipping lanes. The highest density of reports is found within 3 degrees of the coast and north of 30°N latitude. Significant temporal bias may exist, since approximately 50% of the total available observations have been taken since 1945. Nevertheless, the coherence of the resulting vector and scalar fields indicates that our composite distributions can be used to describe the dominant seasonal cycles in upwelling related processes. Moreover, comparisons between our monthly sea surface temperature fields and those of Robinson and Bauer (1971), for example, show good correlation.

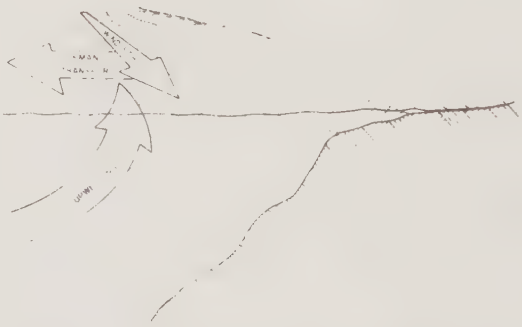


FIGURE 2. A conceptual diagram of the coastal upwelling process. The coast of the continent is represented in cutaway view with the ocean to the left of the figure. Offshore transport in the surface Ekman layer of the ocean due to stress of the wind is replaced by upwelling from depth.

In a simplified view of the coastal upwelling process, equatorward wind stress parallel to the coast induces flow in the surface layers of the ocean which is deflected offshore by the earth's rotation (Figure 2) When this occurs over a wide expanse of coast where longshore horizontal surface flow cannot compensate for that driven offshore, the balance is maintained by upwelling of deeper water. Wooster and Reid (1963) approximated the wind-driven offshore flow as Ekman transport and showed that this "index of upwelling" explained in general the observed features of coastal upwelling in broad diffuse eastern boundary currents such as exists off Baja California.

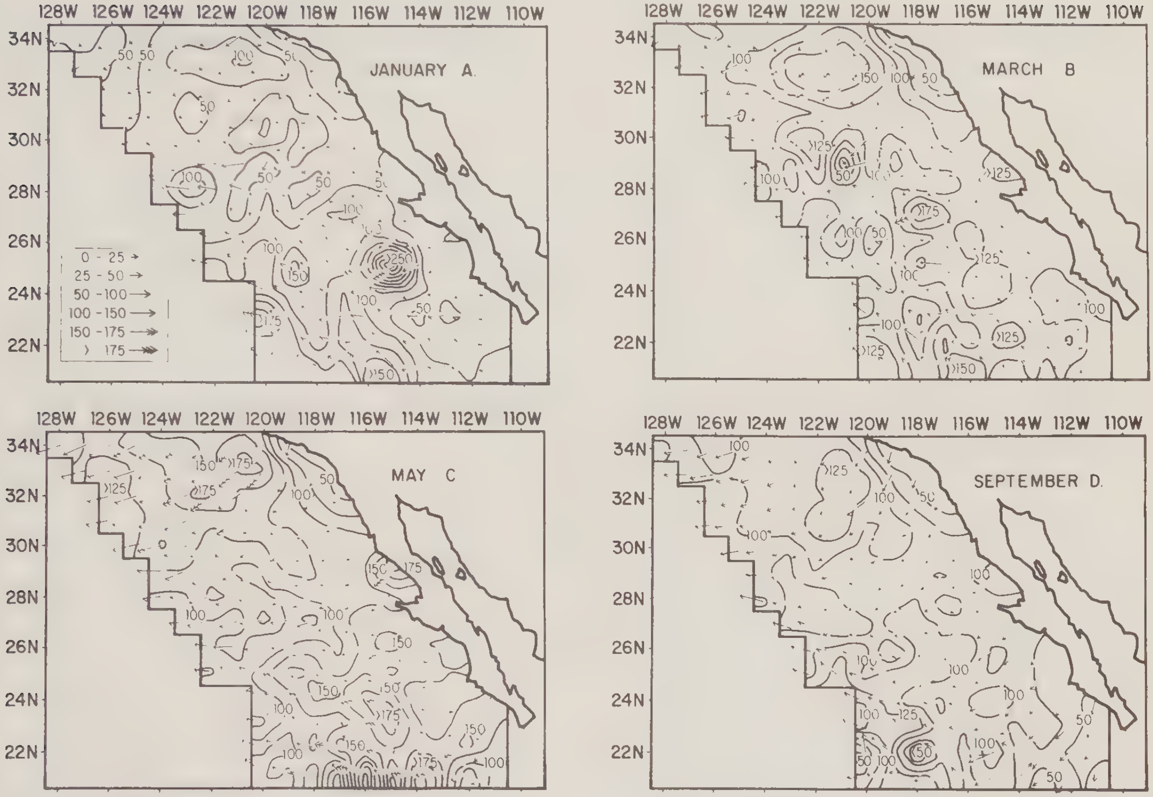


FIGURE 3. Sea surface wind stress. Monthly composite fields of resultant vectors were summarized by 1 degree squares from historical ship observations for A. JANUARY, B. MARCH, C. MAY, and D. SEPTEMBER. Units are dynes/cm². Magnitudes are contoured at intervals of 0.5 dynes/cm². Vector symbols are scaled according to the key.

Wind Stress

In producing the long term composite monthly sea surface wind-stress distributions (Figure 3), the stress was calculated from each wind velocity report according to

$$\tau = \rho_a C_D |\vec{v}| \vec{v} \qquad (1)$$

where:

$\vec{\tau}$ denotes the stress vector

ρ_a is the density of air which was considered to have a constant value of 0.00122 g/cm³

$|\vec{v}|$ is the observed wind speed

$\vec{v}$ is the observed wind velocity vector

C_D is an empirical drag coefficient.

A constant drag coefficient of 0.0016 (Denman and Miyake, 1973) was employed.

The fields show the tendency for an equatorward component of stress to parallel the coast of Baja California, which implies conditions favorable for upwelling throughout the year. Most of the seasonal variability appears in magnitude rather than in direction. A wind stress maximum appears south of Point Conception in March. During May (Figure 3C), stress exceeds 1.0 dyne/cm² within the region north of 30°N latitude, while values for most of the offshore region to the south lie between 0.5 and 1.0 dyne/cm². The maximum immediately north of Punta Eugenia is a consistent feature during the spring. The mean distributions for January and September (Figures 3A and 3D) indicate relaxed conditions. Typical values of surface stress are less than 0.5 dyne/cm². A region of minimum wind stress is indicated along the coast from Point Conception to Punta Banda. This feature corresponds in location to the cyclonic eddy which dominates the ocean surface circulation in the Southern California Bight (Reid, Roden, and Wyllie, 1958).

Surface Wind Transport

Our estimates of the transport in the surface layer of the ocean due to the stress of the wind are based on Ekman's (1905) theory which leads to the following equation for the total integrated mass transport of pure drift currents:

$$\vec{V}_E = \frac{1}{f}\vec{\tau} \times \vec{k} \qquad (2)$$

where:

$\vec{V}_E$ is the total mass transport resulting from an applied local wind stress

f is the Coriolis parameter

$\vec{k}$ is a unit vector directed vertically upward

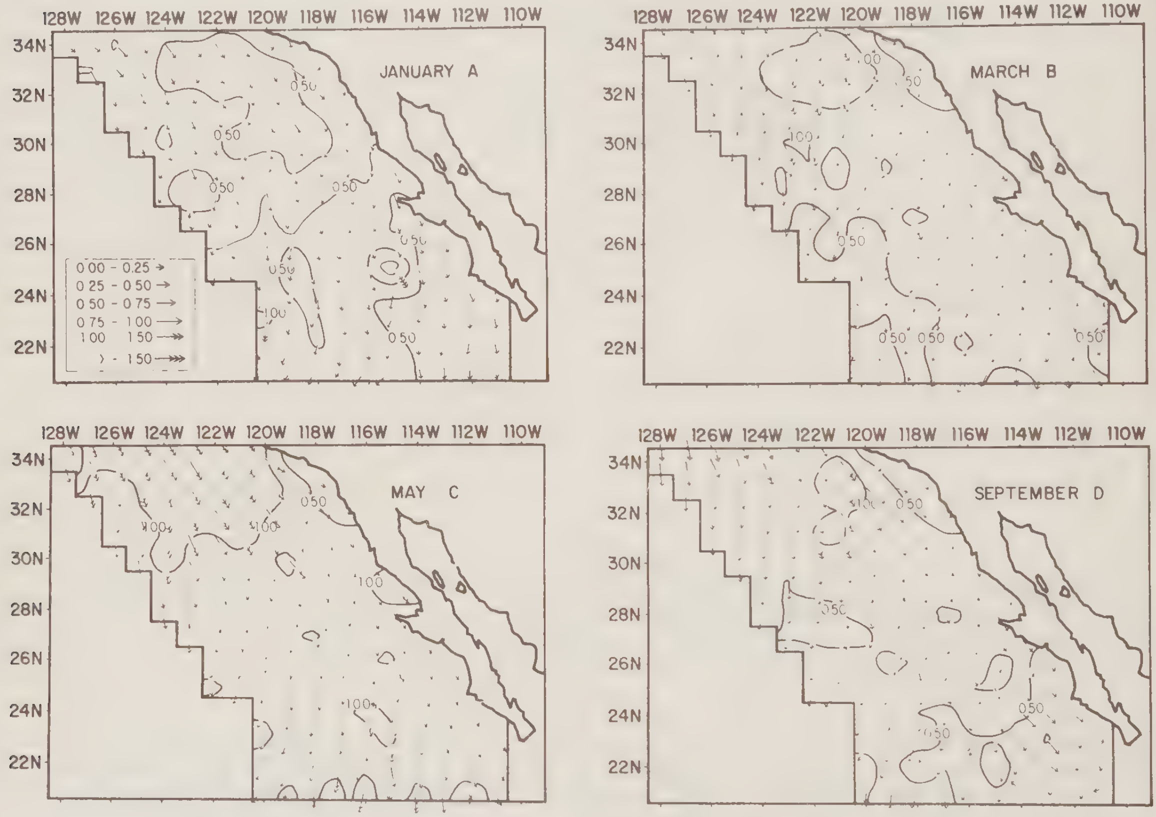


FIGURE 4. Surface Ekman transport. Monthly composite fields of resultant vectors were summarized by 1 degree squares from historical ship observations for A. JANUARY, B. MARCH, C. MAY, and D. SEPTEMBER. Units are metric tons per second per 100 meters coastline. Magnitudes are contoured at intervals of 25 units. Vectors symbols are scaled according to the key.

The relationship implies that the integrated transport is directed 90° to the right of the wind stress in the northern hemisphere.

Composite monthly fields of Ekman transport (Figure 4) were calculated by applying equation (2) to the mean distributions of surface wind stress. The mean transport is directed offshore throughout the year. Accordingly, our conceptual model (Figure 2) indicates strong upwelling in regions of coastal divergence in March and May (Figures 4B and 4C). During these months local maxima in the surface transport appear north of 30°N latitude, immediately north of Punta Eugenia, and south of 24°N, where the decrease in the Coriolis parameter leads to corresponding increases in the computed Ekman transport. Offshore gradients in the surface transport may contribute to convergences and divergences, thereby altering the distributions of organisms.

The seasonal cycle of Ekman transport (Figures 5 and 6) within the selected 1-degree squares adjacent to the coast (Figure 1) indicates the general seasonal pattern of local wind forcing of coastal upwelling. The degree of correspondence in general shape and position of the contours of absolute magnitude in the vector time series (Figure 5) with the contours of magnitude of the offshore component (Figure 6) illustrates the primarily offshore direction of wind driven surface flow off Baja California, implying some degree of upwelling on average throughout the year. Strongest upwelling appears to occur from March to June, and along the coast from 20°N to 30°N.

A maximum is apparent north of Punta Eugenia at 28°N latitude. From September to December, offshore transport weakens, and changes sign in September at 21°N. July and August, and January and February appear to be transition periods.

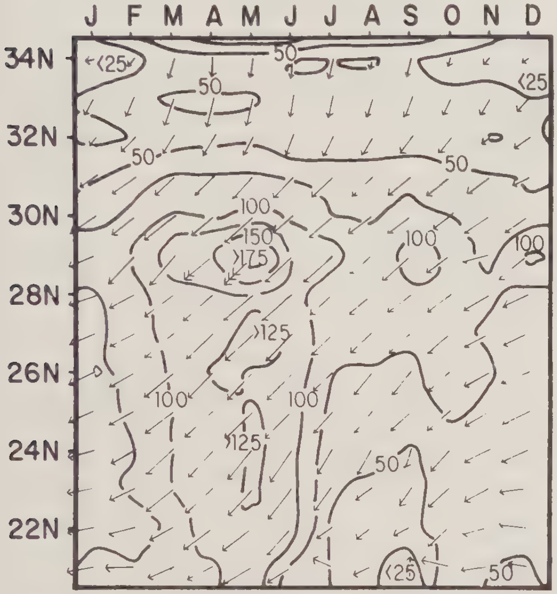


FIGURE 5. Seasonal cycle of Ekman transport near the coast. Resultant vectors were summarized by month for the group of selected 1 degree squares adjacent to the coast shown in Figure 1. Units are metric tons per second per 100 m coastline. Magnitudes are contoured at intervals of 25 units. Vector symbols are scaled according to the key in Figure 4A.

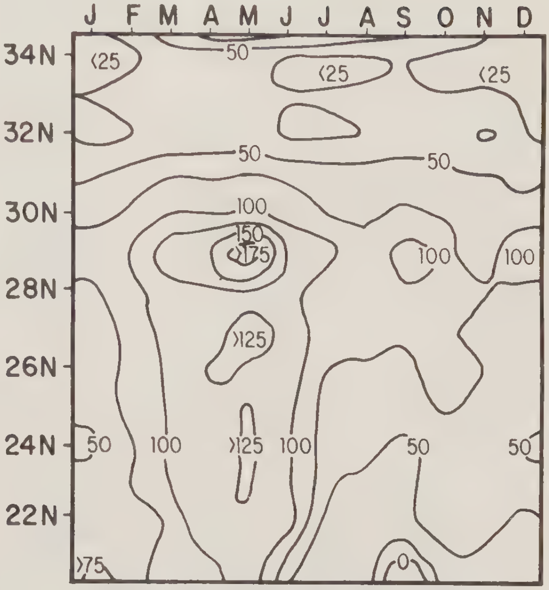


FIGURE 6. Seasonal cycle of offshore Ekman transport. Means of offshore components of Ekman transport were computed by month within the group of selected 1 degree squares near the coast shown in Figure 1. Units are metric tons per second per 100m coastline. Onshore Ekman transport is shaded.

In addition to the surface Ekman wind drift, the ocean surface flow field also contains geostrophic components. Sverdrup, Johnson, and Fleming (1942, page 501) describe a linkage by which the accumulation of denser upwelled water near the coast and the transport away from the coast of lighter surface water leads to a redistribution of mass. The balance between the resulting pressure gradient and the Coriolis force produces a geostrophic current in the equilibrium state. Consequently, on a seasonal basis, one might expect variations in the offshore component of Ekman transport to be well correlated with variations in longshore flow. Indeed, investigators in CUEA have demonstrated this correspondence on shorter time scales (Huyer, et al., 1974).

Surface Currents

The only available direct measurements of ocean surface flow having reasonable spatial and seasonal coverage are reports of drift attributed to ocean currents, compiled from ships' log books. We have made seasonal summaries from the ship drift file of the U.S. Naval Oceanographic Office. These data are much the same as used by Wyrtki (1965). The density of available reports is only about one-tenth that of marine surface observations and is dependent upon the primary coastwise shipping lanes. Significant bias by month and year is apparent; March, May, and November contain approximately two to four times as many observations as any other month, and most of the observations were reported prior to 1940.

Ship drift distributions are inherently noisy and require a large data base to resolve the underlying patterns. To increase the number of observations per averaged value, we have used summaries by 2-degree squares, by month (Figures 7 and 8), and by quarter (Figure 9). The precise interpretation of these measurements remains open to question since wind effects on reporting vessles are indeterminate. However, Stidd (1974) has indicated a closer correspondence of ship drift to ocean current direction than to wind direction. In addition, mean ship drift vectors are in some cases directed oppositely to mean wind vectors. The Southern California Countercurrent is an example.

A significant correlation between the longshore component of surface current (Figure 8) and the offshore component of Ekman transport (Figure 6) is apparent. Specifically, during the period of maximum offshore transport, equatorward surface flow in the California Current is strongest. Indeed, there is a correspondence between the position of

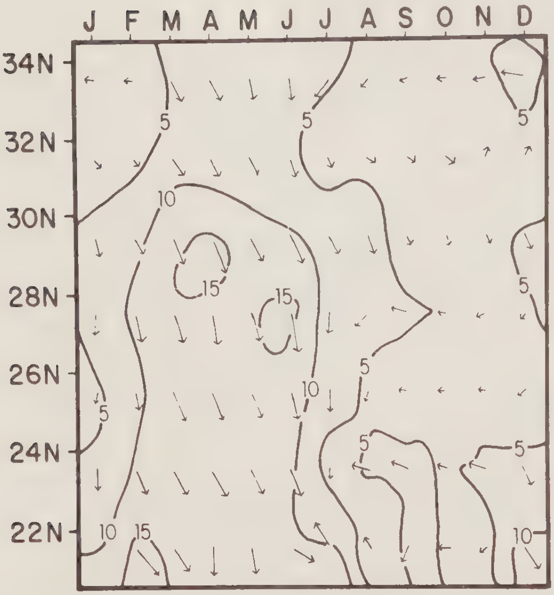


FIGURE 7. Seasonal cycle of ship drift near the coast. Resultant vector were summarized by month from the NAVOCEANO ship drift file, for a group of 2 degree squares along the coast from latitude 20°N to 34°N. Units are cm/sec. Magnitudes are contoured at intervals of 5 cm/sec. Vector symbols are scaled according to the key in Figure 9A.

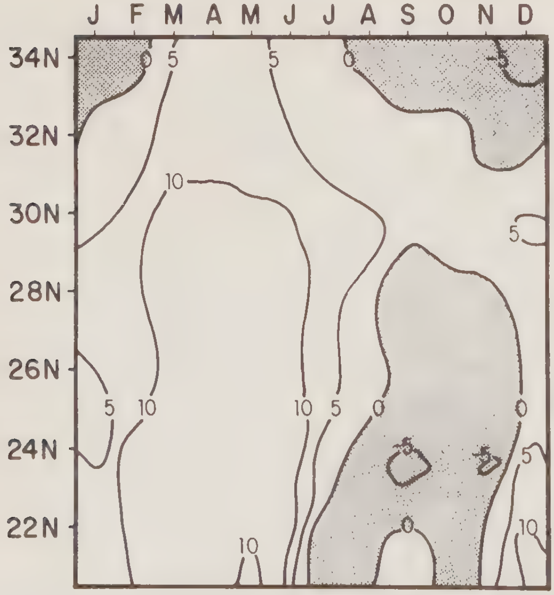


FIGURE 8. Seasonal cycle of longshore ship drift. Means of components parallel to the coast were summarized from the NAVOCEANO ship drift file for a group of 2 degree squares along the coast from latitude 20°N to 34°N. Units are cm/sec. Positive values indicate equatorward drift. Poleward drift is shaded.

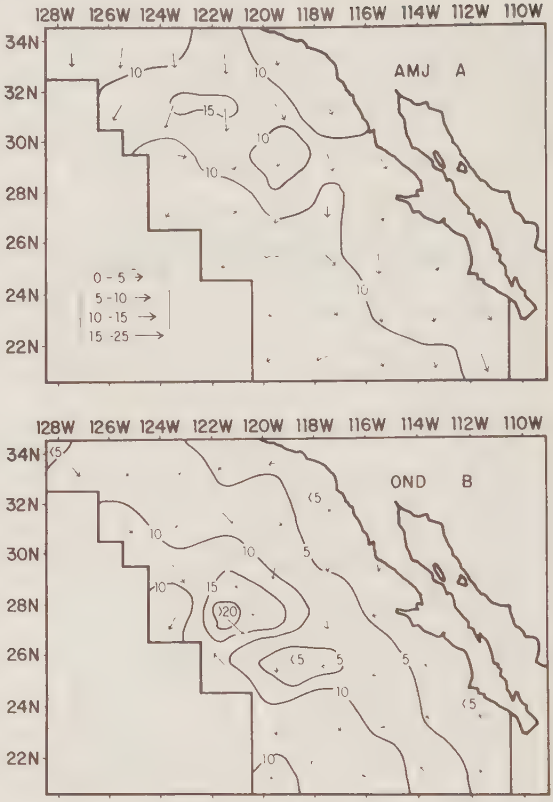


FIGURE 9. Ship drift. Composite field of resultant vectors were summarized by quarter and by 2 degree squares from the NAVOCEANO ship drift file for A. APRIL-MAY-JUNE and B. OCTOBER-NOVEMBER-DECEMBER. Units are cm/sec. Magnitudes are contoured at intervals of 5 cm/sec. Vector symbols are scaled according to the key.

the maximum offshore Ekman transport north of Punta Eugenia (Figure 5) and the position of the strongest longshore surface currents at latitude 29° N in April and May (Figure 7). During the relaxed period of upwelling, from September to December, the surface current changes direction and flows offshore, but has a definite poleward component along the coast. The surface current data indicate cyclonic flow in the Southern California Bight, where offshore Ekman transport is less than 50 metric tons per second per 100 m of coastline throughout the year. These data suggest that the surface countercurrent off Baja California may only form where offshore Ekman transport is weak.

During the spring upwelling season, surface current parallels the coast with only a slight offshore component (Figure 9A) and reaches a maximum strength of about 15cm/sec (Figure 7). During the period of relaxed upwelling, the current changes direction and slows to less than 5 cm/sec (Figure 9B). Flow is primarily offshore, but there is some suggestion of a coastal countercurrent. The lack of coherence in the distributions between 7 and 10 degrees off the coast reflects scarcity of data.

Sea Surface Temperature

Vertical and horizontal advection associated with coastal upwelling alter the patterns of surface isotherms which are approximately zonally distributed off Baja California. The composite surface temperature field for June (Figure 10) shows cold water indicative of upwelling along the coast from Punta Eugenia to Punta Baja. This feature correlates well with the local Ekman transport maximum in the same area. South of latitude 25° N, indications of upwelling in the temperature distribution are slight. In the region off southern California, the warm coastal temperatures may reflect seasonal heating and warm advection in the cyclonic eddy (Reid, Roden, and Wyllie, 1958).

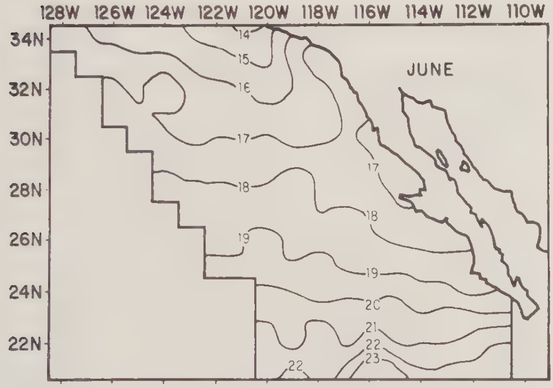


FIGURE 10. Sea surface temperature during June. Mean values of sea surface temperature observations were computed by 1 degree squares for the month of June. Units are degrees Celsius.

The coarse resolution in the 1-degree spatial summaries used in this paper tends to mask fine scale features of the temperature distributions. These particular temperature fields were developed to be compatible in resolution to, and used in conjunction with, our other data fields. More detailed treatments can be found in California Marine Research Committee (1963), Lynn (1967), and Wyllie and Lynn (1971).

The seasonal cycle of the sea surface temperature offshore (Figure 11) shows a normal north-south temperature gradient and a seasonal warming-cooling cycle with a typical range of 2° C to 4° C. Minima occur from February to March and maxima from August to September.

Comparison of the temperature cycle near the coast (Figure 12) with that occurring offshore (Figure 11) shows differences which may be largely

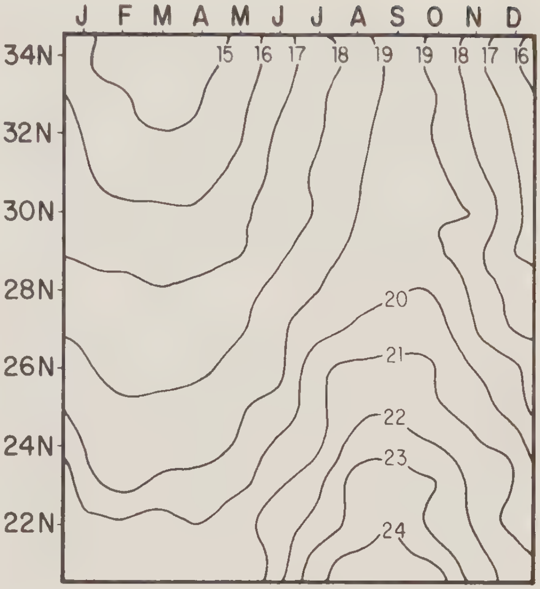


FIGURE 11. Seasonal cycle of sea surface temperature in the offshore region. Mean values of sea surface temperature observations were computed by month for the group of selected 1 degree squares indicated in Figure 1 at the offshore edge of the grid. Units are degrees Celsius.

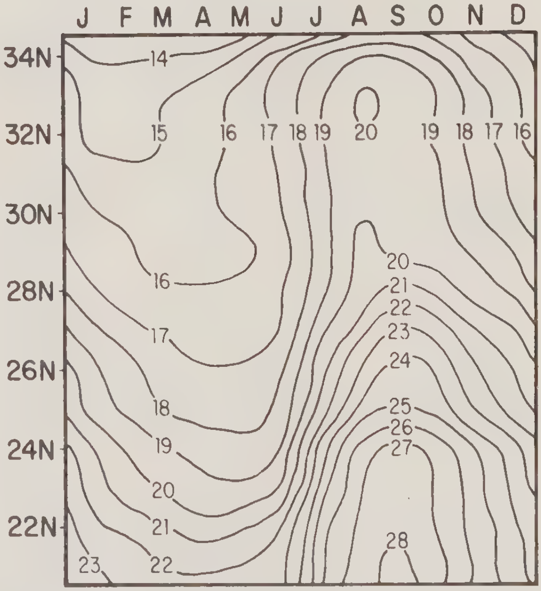


FIGURE 12. Seasonal cycle of sea surface temperature near the coast. Mean values of sea surface temperature observations were computed by month for the group of selected 1 degree squares adjacent to the coast, indicated in Figure 1. Units are degrees Celsius.

attributable to the effect of coastal upwelling, and to differences between horizontal advection in the offshore region and that in the coastal region. There is also the possibility of significant spatial differences in ocean-atmosphere heat exchange. Near the coast the seasonal temperature minimum is delayed relative to that offshore, occurring from March to May in phase with the maximum offshore Ekman transport. A more rapid increase of temperature near the coast during early summer, corresponding to the weakening of the southward surface flow (Figure 7), leads to significantly higher temperatures near the coast during summer than at the same latitude offshore.

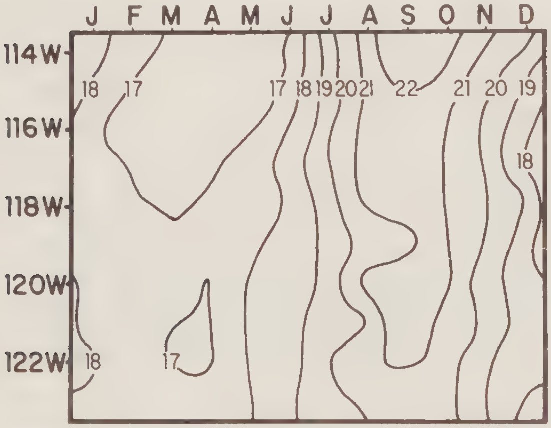


FIGURE 13. Seasonal cycle of sea surface temperature off Punta Eugenia. Mean values of sea surface temperature observations were computed by month for the group of selected 1 degree squares extending westward from the coast south of Punta Eugenia, indicated in Figure 1. Units are degrees Celsius.

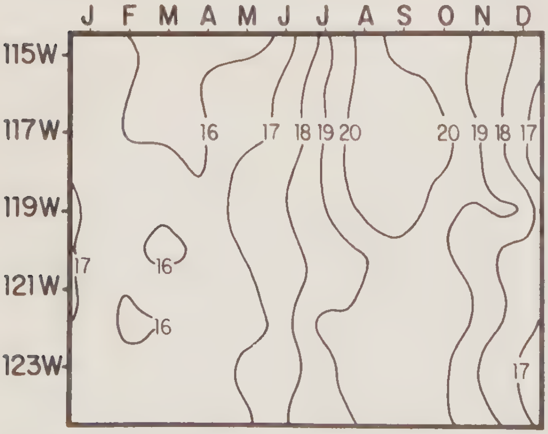


FIGURE 14. Seasonal cycle of sea surface temperature off Punta Baja. Mean values of sea surface temperature observations were computed by month for the group of selected 1 degree squares extending westward from the coast south of Punta Baja, indicated in Figure 1. Units are degrees Celsius.

Time series displays of seasonal sea surface temperatures in lines of squares extending westward from the coast (Figures 13 and 14) show colder water appearing near the coast in March. The gradients extend several hundred kilometers offshore during spring. During early summer, advection and possible spatial variations in ocean-atmosphere heat exchange processes offset the upwelling indicated by a continued, although weakened, offshore Ekman transport (Figure 6), leading to nearly homogeneous temperatures in the offshore direction. By late summer, warmer advection near the coast relative to that occurring offshore appears to dominate. Warm temperatures are found near the coast; gradients extend hundreds of kilometers offshore. During late fall and winter southward flow begins to increase (Figure 8) and the offshore temperature distribution again becomes nearly homogeneous (Figures 13 and 14).

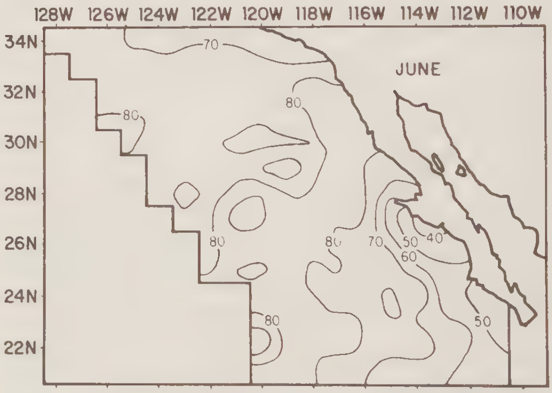


FIGURE 15. Cloud cover during June. Means of reported cloud amounts were computed by 1 degree squares during the month of June. Units are percent of sky obscured.

Cloud Cover

Seasonal and spatial variations in the heat exchange may mask features of upwelling normally evident in distributions of sea surface temperature. In the composite field of total cloud cover for June (Figure 15), Punta Eugenia separates an area of minimum cloud cover along the coast (less than 50%), from an area of maximum cloud cover (greater than 80%). A change in total cloud cover from 40% to 80% could result in a relative decrease of more than 30% in the incident radiation (Seckel and Beaudry, 1973) with corresponding changes in the sea surface temperature.

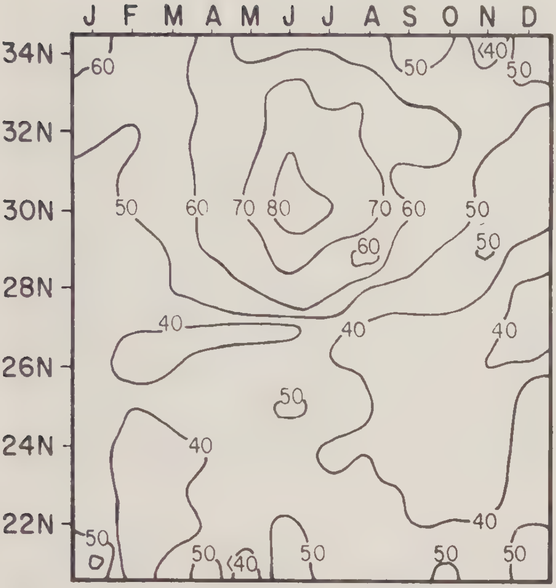


FIGURE 16. Seasonal cycle of cloud cover near the coast. Mean values of reported cloud amounts were computed by month for the group of selected 1 degree squares adjacent to the coast, indicated in Figure 1. Units are percent of sky obscured.

Considering the seasonal variations in cloud cover within the longshore section of coastal squares (Figure 16), maximum cloud cover appears to be associated with the upwelling off Punta Baja, while minimum cloud cover is evident along the entire coast south of Punta Eugenia. When distributions of cloud cover for sections extending westward from the coast are considered (Figures 17 and 18), the section off Punta Eugenia indicates minimum cloud cover at the coast throughout the year, while relative maxima occur at the coast in the Punta Baja section during June and July. The data suggest that differences in the downward flux of radiation associated with these cloud cover distributions could lessen the indications of coastal upwelling in the sea temperature south of Punta Eugenia. To the north, however, the heat flux from the atmosphere during the upwelling season may be insufficient to obscure the effects of cold water upwelled into the surface layer.

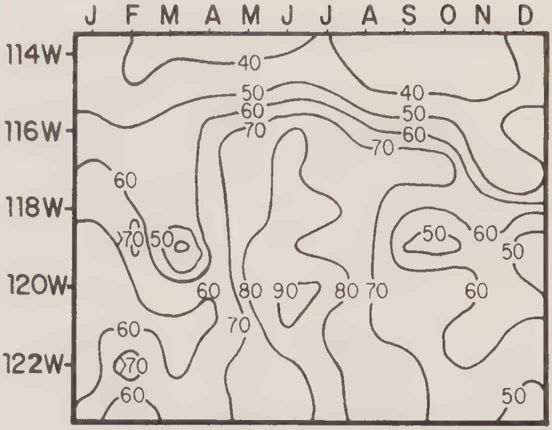


FIGURE 17. Seasonal cycle of cloud cover off Punta Eugenia. Mean values of cloud cover observations were computed by month for the group of selected 1 degree squares extending westward from the coast south of Punta Eugenia, indicated in Figure 1. Units are percent of sky obscured.

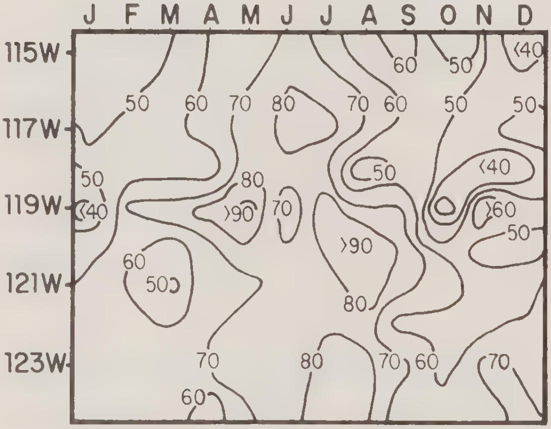


FIGURE 18. Seasonal cycle of cloud cover off Punta Baja. Mean values of cloud cover observations were computed by month for the group of selected 1 degree squares extending westward from the coast south of Punta Baja, indicated in Figure 1. Units are percent of sky obscured.

Wind Stress Curl

Although coastal upwelling occurs only at the ocean boundary, wind-induced upwelling can occur whenever divergence in the surface wind drift is not compensated by other modes of horizontal surface flow. The divergent or convergent nature of the surface Ekman wind drift offshore of the primary coastal upwelling zones is determined by the wind stress curl (Figure 19). If the equatorward wind stress parallel to the coast increases in the offshore direction, a situation characterized by positive curl in the stress field, the offshore component of Ekman transport likewise increases in the offshore direction. The result is continued divergence offshore requiring upwelling to maintain the mass balance. Conversely, if the equatorward longshore wind stress decreases in the offshore direction, the wind stress curl is negative. The result is convergence in the surface wind drift with corresponding frontal formation and downwelling.

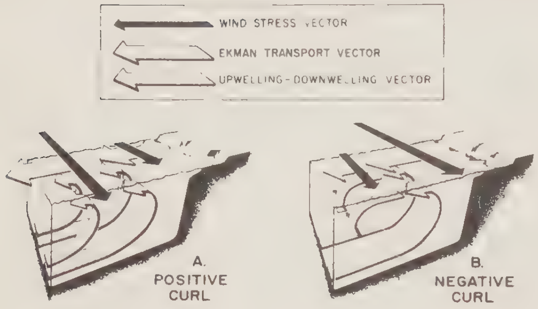

WIND STRESS VECTOR
EKMAN TRANSPORT VECTOR
UPWELLING-DOWNWELLING VECTOR
A. POSITIVE CURL
B. NEGATIVE CURL

FIGURE 19. A conceptual diagram of the relationship of wind stress curl to divergence and convergence of surface Ekman transport offshore of the primary coastal upwelling zone. An increase in the equatorward wind stress parallel to the coast (positive wind stress curl) produces divergence in surface Ekman transport and continued upwelling offshore. A decrease in the equatorward wind stress parallel to the coast (negative wind stress curl) produces convergence in surface Ekman transport and downwelling offshore.

Actual observations of wind stress curl are not available. Alternatively, we have computed the curl of the mean wind stress fields under the assumption that, since the curl is a linear operator, the resulting distributions may resemble mean fields of actual wind stress curl distributions existing off Baja California. Monthly curl fields corresponding to the mean wind stress distributions (Figure 3) were determined (Figure 20). Negative wind stress curl (Ekman convergence) is characteristic of the offshore region. From Punta Baja to Punta Eugenia the convergent region reaches to the coast. The wind stress distributions thus imply favorable conditions for formation of fronts and convergent patches of recently upwelled water in this area. North of Punta Baja and south of Punta Eugenia areas of positive curl (Ekman divergence) extend from the coast to several hundred kilometers seaward. Within these divergent areas there would tend to be a continued, although much reduced, level of upwelling offshore of the primary coastal upwelling zone.

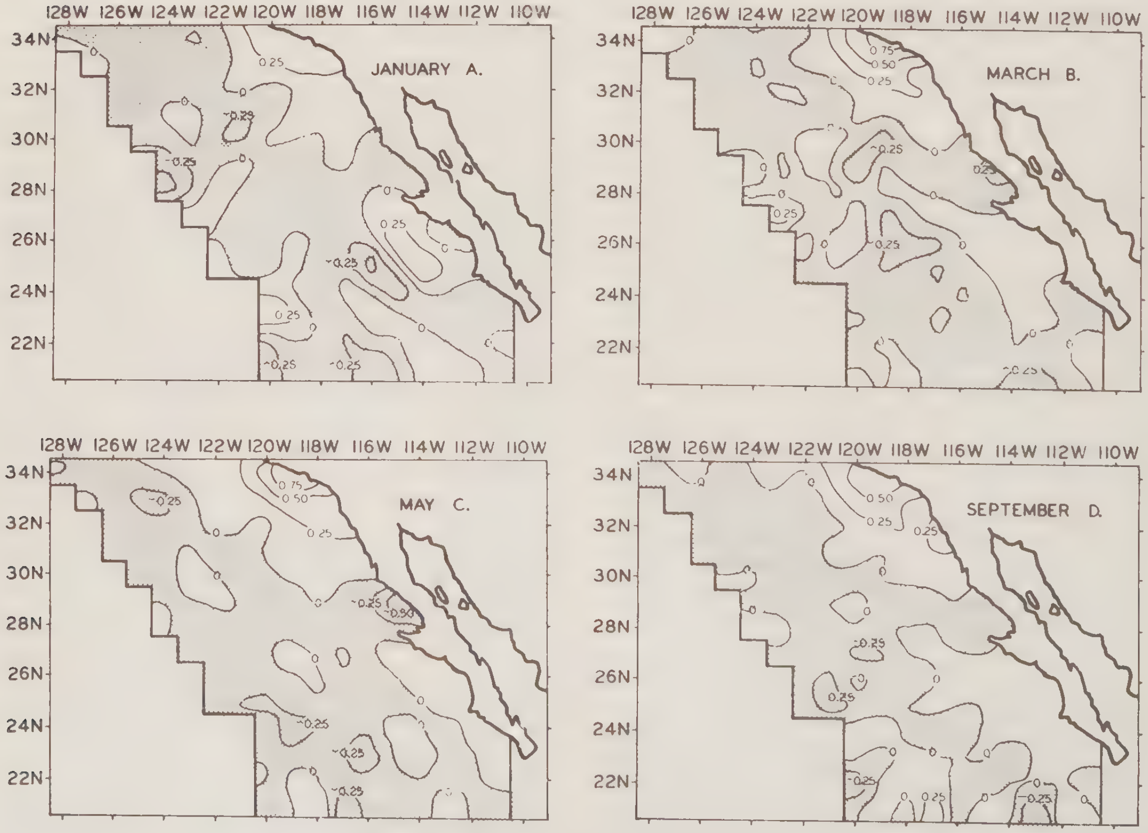

128W 126W 124W 122W 120W 118W 116W 114W 112W 110W
34N 32N 30N 28N 26N 24N 22N
JANUARY A.
MARCH B.
MAY C.
SEPTEMBER D.
0
0.25
-0.25
0.50
0.75

FIGURE 20. Wind stress curl. Monthly composite fields of wind stress curl were computed from the surface wind stress fields shown in Figure 3; A. JANUARY, B. MARCH, C. MAY, and D. SEPTEMBER. Units are dynes/cm²/100km. The coutour interval is 0.25 dynes/cm²/100 km. Negative values are shaded.

Munk (1950) has suggested that the poleward undercurrent observed along the California coast may be a consequence of the local wind stress curl. Pedlosky (1974) has indicated theoretically that a poleward undercurrent would be favored by positive wind stress curl along the coast and a poleward decrease in the surface heating. The surface data presented here cannot describe features of the subsurface flow. However the mean wind stress distributions off the coast appear generally consistent with a pattern of countercurrent inshore and equatorward flow offshore, except in the region from Punta Eugenia to Punta Baja where the wind stress curl is not positive. During the fall, the relaxation of upwelling induced equatorward surface flow would favor surfacing of a coastal countercurrent. With these considerations in mind it is interesting to note that indications of a poleward component of ship drift during fall (Figure 9B) are lacking in the region from Punta Eugenia to Punta Baja. Rather, the data suggest separate cyclonic gyres in the regions of positive wind stress curl off the Los Angeles Bight and south of Punta Eugenia.

VARIABILITY AND PERSISTENCE

In addition to responding to the seasonal variations, marine biological communities must also respond to a wide spectrum of environmental variations of time scales ranging from many years to small fractions of a year. A central problem in investigating such fluctuations is the formation of consistent time series of pertinent information.

For any particular synoptic sampling the available reports from ships at sea tend to be sparse and unevenly distributed. In such a situation the variability introduced by random errors in measurement or changes in spatial distribution of reports may be as great or greater than the variability in the process itself. If a definite periodicity is known it may be reasonable to composite corresponding portions of different cycles, as was done in the previous section, in order to obtain an adequate data base. This is not possible in the case of fluctuations which are nonperiodic or where, if they do contain periodic components, the periodicities are undefined.

One way to arrive at fairly consistent time series of wind information with which to investigate fluctuations in upwelling is to make use of analyzed products produced by meteorological agencies. In this section we use 6-hourly computations of offshore Ekman transport based on the synoptic surface atmospheric pressure analyses produced by Fleet Numerical Weather Central. These analyses incorporate all available wind reports in the form of equivalent pressure gradients as well as the available pressure data (Holl and Mendenhall, 1972). Conventional reporting periods correspond to 4AM, 10AM, 4PM, and 10PM Pacific Standard time, yielding four synoptic samplings per day.

Bakun (1973) described a procedure for computing offshore Ekman transport from pressure fields using a geostrophic wind computation and a simplified boundary layer approximation. The results of such computations were called *upwelling indices.* A compilation of daily and weekly means of 6 hourly indices at 15 locations off western North America has been published (Bakun, 1975). The time series discussed in this paper are located at five 3 degree grid intersections, from 21°N to 33°N latitude (Figure 1).

This 3 degree resolution is coarse compared to the 1 degree resolution achieved in the previous section. The pressure fields were originally analyzed on a grid of approximately 3 degree mesh length. Thus any information derived on a smaller scale would consist merely of the details of the particular interpolation function used, rather than having any basis in observed data. Underlying this situation is the fact that the number of reports from the area off Baja California during any synoptic period is only of the order of one per 3 degree square and so analysis of pressure on a smaller scale grid would not increase the resolution of data-based information.

The drag coefficient used in equation (1) to compute these indices was 1.3×10^{-3}. This differs from the value 1.6×10^{-3}, based on the work of Denman and Miyake (1973), used in the previous section. Recent progress in the field of ocean-atmosphere boundary processes suggests that 1.3×10^{-3} may be a more appropriate constant value.

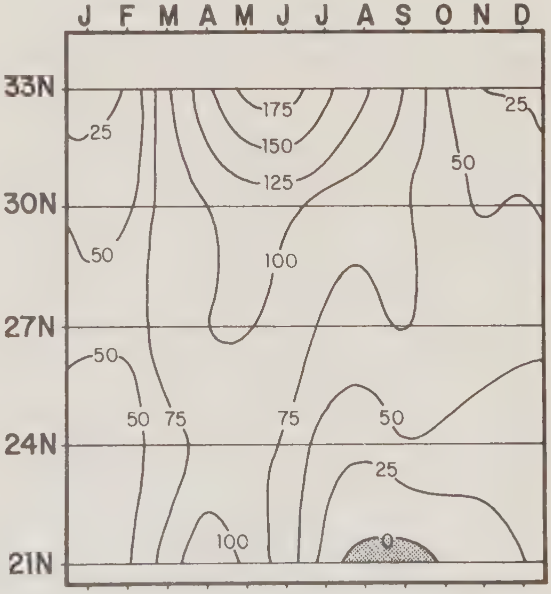


FIGURE 21. Mean values by month and position of 6 hourly coastal upwelling indices for the 7 year period, 1967–73. Locations are indicated by large dots in Figure 1. Units are m³ per second per 100 m of coast. Negative values are shaded.

Actually the drag coefficient appears to vary both with atmospheric stability and with spectral properties of the ocean waves (Davidson, 1974), but the form of the dependencies does not appear well enough established to warrant incorporation of these effects for our purposes. Since the drag coefficient enters linearly into the computations of stress and Ekman transport, the values in the previous section could be adjusted to those of this section by multiplication by the factor 1.3/1.6 = 0.8125. Because of such uncertainties, these results, although yielding reasonably realistic numerical values, should properly be viewed as being "uncalibrated" in terms of absolute quantitative detail. The uncertainty in magnitudes is more severe in the case of indices computed from analyzed pressure fields.

Comparison of the 7 year (1967–73) mean values of the 6 hourly upwelling indices (Figure 21) to the seasonal cycle of offshore Ekman transport composited on a 1 degree basis from actual ship reports (Figure 6) illustrates the smoothing of gradients and other spatial details on the 3 degree synoptic index format. It also illustrates a severe spatial distortion in absolute magnitudes discussed by Bakun (1973) which results in amplification of the computed indices at 33°N latitude relative to those at points further south. The figures in this paper which display absolute magnitudes of computed upwelling indices are intended to indicate temporal variations, i.e. relationships along the horizontal axis of the figures. Contours are connected between different locations only as a visual aid and to indicate variations in seasonal timing between different locations. Comparisons of absolute magnitudes on the vertical axis can be misleading. In the case of normalized properties such as skewness and kurtosis the problem is less severe.

Properties of Fluctuations

High variance in the 6-hourly computed indices tends generally to correspond in season and location to high mean value (Figure 22). Thus the winter season is characterized by a generally relaxed level of activity and thus a more stable upwelling regime. Two variations from the pattern are noticeable. At 21°N latitude where during late summer the mean goes negative, i.e. downwelling occurs on average, there is a relative maximum in the variance. Thus the low mean absolute values must reflect a near cancellation of contributions to the variance by large positive and negative fluctuations. Off central Baja California where there are double peaks in the mean, the larger occurring in spring and the lesser in late summer, the late summer period exhibits the greater variance.

Skewness of the monthly distributions is generally positive (Figure 23). Thus the strong departures from the mean are most often spikes of even more intense upwelling separated by longer relaxed periods rather than an equal mix of fluctuations above and below the norm. Highly skewed distributions are at 21°N latitude during the spring

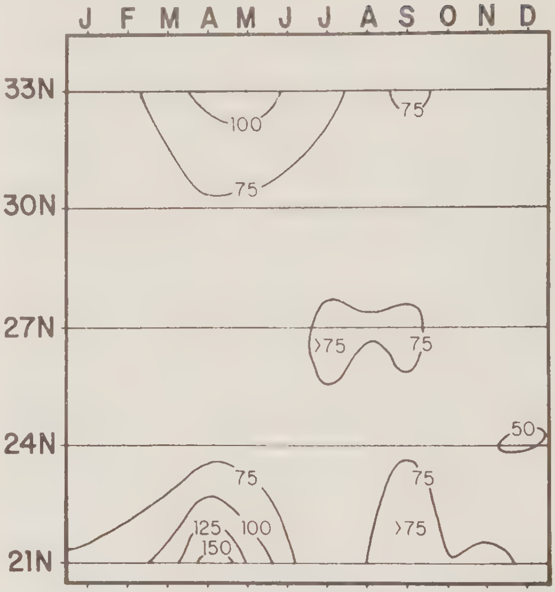


FIGURE 22. Standard deviations of monthly distributions of 6 hourly coastal upwelling indices. Locations are indicated by large dots in Figure 1. Units are m³ per second per 100 m of coast. Period covered is 1967–73.

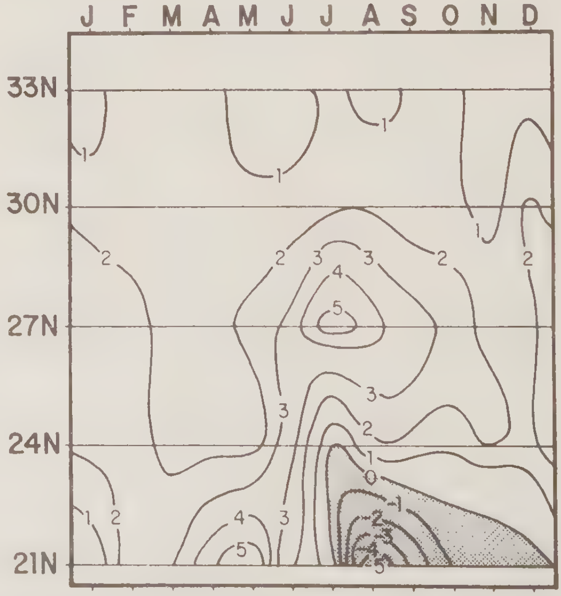


FIGURE 23. Skewness of monthly distributions of 6 hourly coastal upwelling indices. Locations are indicated by large dots in Figure 1. Period covered is 1967–73. Negative values are shaded.

upwelling maximum and off Central Baja California during the relative minimum which separates the spring and late summer maxima. The skewness turns negative during late summer and fall at 21°N. The area of negative skewness extends to 24°N during July and corresponds to a similarly shaped region of low mean monthly values of the indices (Figure 21). This situation appears to be one of fairly consistent low level upwelling interrupted at infrequent intervals by downwelling events of such an intensity as to nearly cancel the upwelling on average. The mean actually goes negative at 21°N during August and September. These downwelling events probably reflect the occurrence of tropical storms.

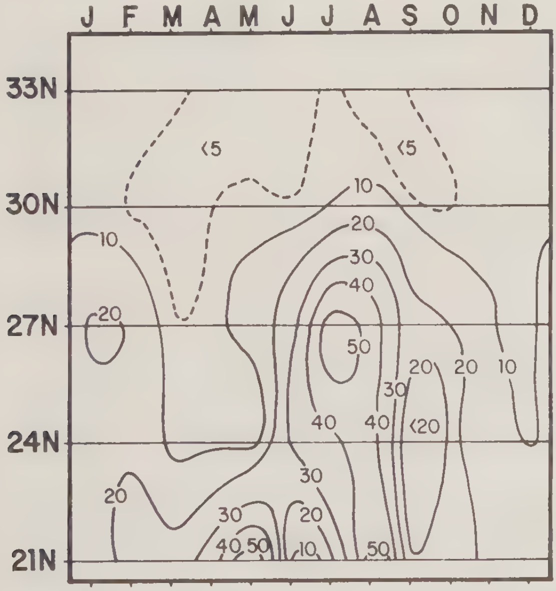


FIGURE 24. Kurtosis of monthly distributions of 6 hourly coastal upwelling indices. Locations are indicated by large dots in Figure 1. Period covered is 1967–73.

Kurtosis of the monthly distributions is greater than 3.0 at all months and locations indicating larger contributions from extreme events than would be the case in a Gaussian process (Figure 24). Off central and southern Baja California during spring and summer the large variance corresponds to large kurtosis, again indicating the importance of rare, very intense events. In the north the spring and fall seasons of maximum variance are characterized by minimum kurtosis, indicating the variance to be dominated by more frequent, less extreme pulsations.

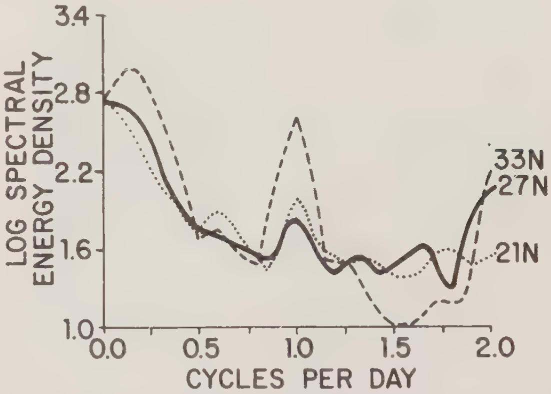


FIGURE 25. Power spectra of 6 hourly coastal upwelling indices. Spectra are plotted for time series at three locations (21°N, 107°W; 27°N, 116°W; 33°N, 119°W) for the period February 27 through July 1, 1972.

Power spectra (Figure 25) were selected as being representative of a number of similar spectra computed for various segments of the 7 year series of 6 hourly indices. The major features, i.e., the strong diurnal peak and a general increase in energy at low frequencies representing seasonal and other long term variations, appear consistently. The indication of a major amount of energy spread over an "event scale" of periods ranging from 2 or 3 days to several weeks is also typical. The spectral peak at the semidurnal frequency reflects the non-sinusoidal shape of the diurnal fluctuation which tends to have a faster rate of change during the morning to afternoon increase than during the evening to morning relaxation.

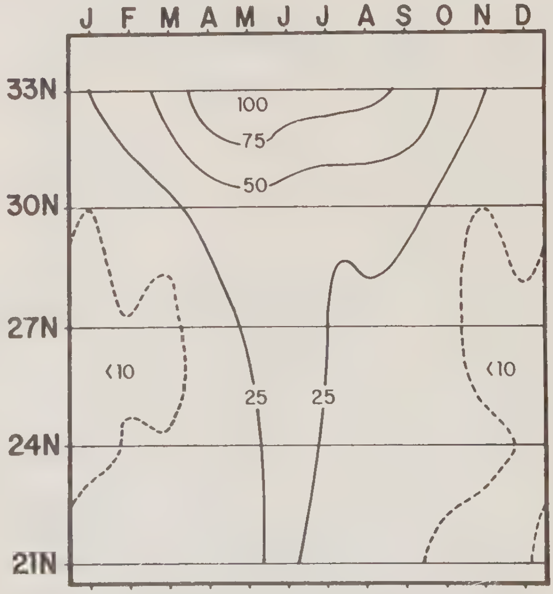


FIGURE 26. Diurnal variation in upwelling indices. Mean differences between upwelling indices computed from the 4 PM Pacific Standard Time synoptic sampling and those computed from the 10 AM sampling 6 hours earlier were computed by month at locations indicated by large dots in Figure 1. These two sampling periods tend to be extremes of the diurnal cycle as resolved by these data. Units are m³ per second per 100 m of coast. Period covered is 1967–73.

The 10AM and 4PM (Pacific Standard Time) synoptic periods tend to be the extremes of the diurnal cycle as well as it can be resolved with the four samples per day available. The mean difference, the afternoon value minus the morning value, is positive at all months and locations (Figure 26). The amplitude tends to be greatest in the late spring and early summer and least in the winter. At 21°N latitude the minimum is earlier than at the locations further north, occuring during the fall. The diurnal variation is greatest at 33°N and is progressively smaller to the south. How much of this apparent north-south gradient in the diurnal effect may be due to the previously mentioned spatial distortion is presently unclear.

The diurnal effect is very apparent in autocorrelation functions produced from upwelling index time series (Figure 27), where the diurnal rise and fall appears superimposed on a strong decline in autocorrelation which occurs within 1 to 2 days. This rapid decline illustrates the characteristically short time scales of the indicated pulses of upwelling producing wind stress.

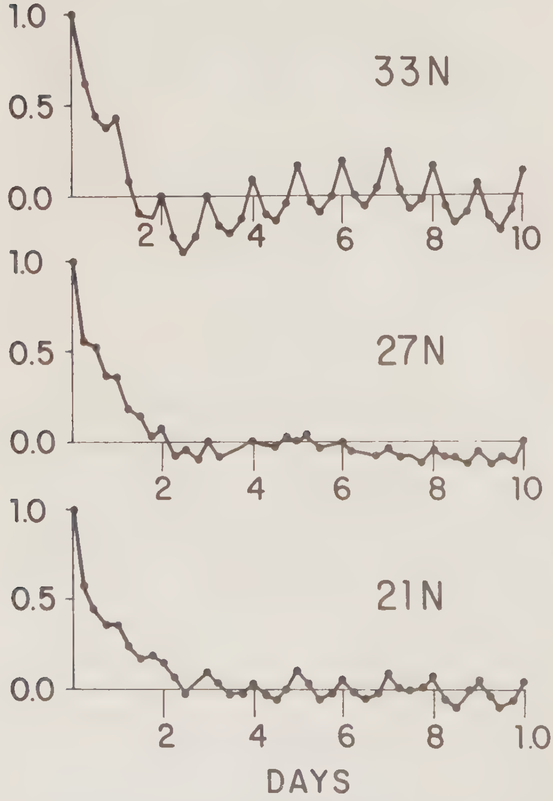


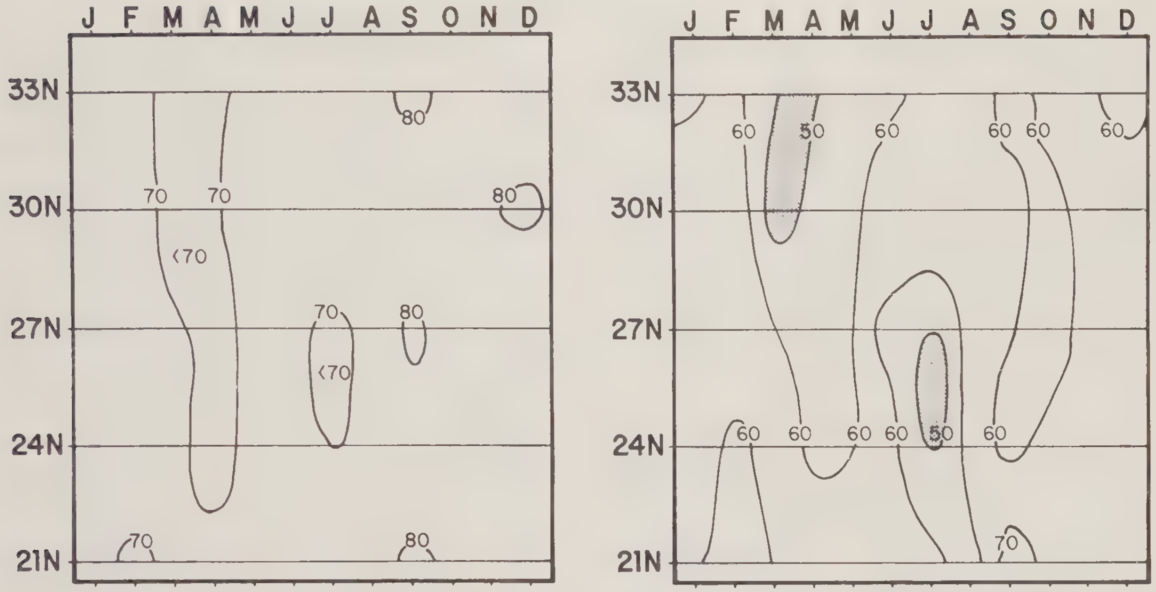
FIGURE 27. Autocorrelation functions for 6 hourly coastal upwelling indices. Functions are plotted for three locations (21°N, 107°W; 27°N, 116°W; 33°N, 119°W) during the period February 27 through July 1, 1972.

Persistence

Characteristic time scales were further examined in terms of persistence of anomalies in the 6 hourly upwelling indices (Figure 28). Since anomalies in these series tend to be much larger than the differences between various types of fits to the annual cycle, mean seasonal values were simply defined by linear interpolation between succeeding months, the midpoints of which were assigned the 7 year composite mean monthly value of the 6 hour upwelling indices. To avoid complicating effects of the diurnal cycle the analysis was done in terms of daily means. An anomaly was defined as the difference between a daily mean value and the value for the particular day from the linearly interpolated mean annual cycle. The percentage of times during the 7 year time series that a daily anomaly had the same sign as the anomaly for the previous day was computed for each month and location (Figure 28A). Situations where the anomaly was so small that it was not significantly either positive or negative were rejected by requiring the previous anomaly to have an absolute value of at least 10 m^3 per second per 100 m of coastline for the particular day to be used in the computation. This process was repeated using the respective anomalies 2, 3, and 5 days earlier in the comparisons (Figure 28B, C, and D).

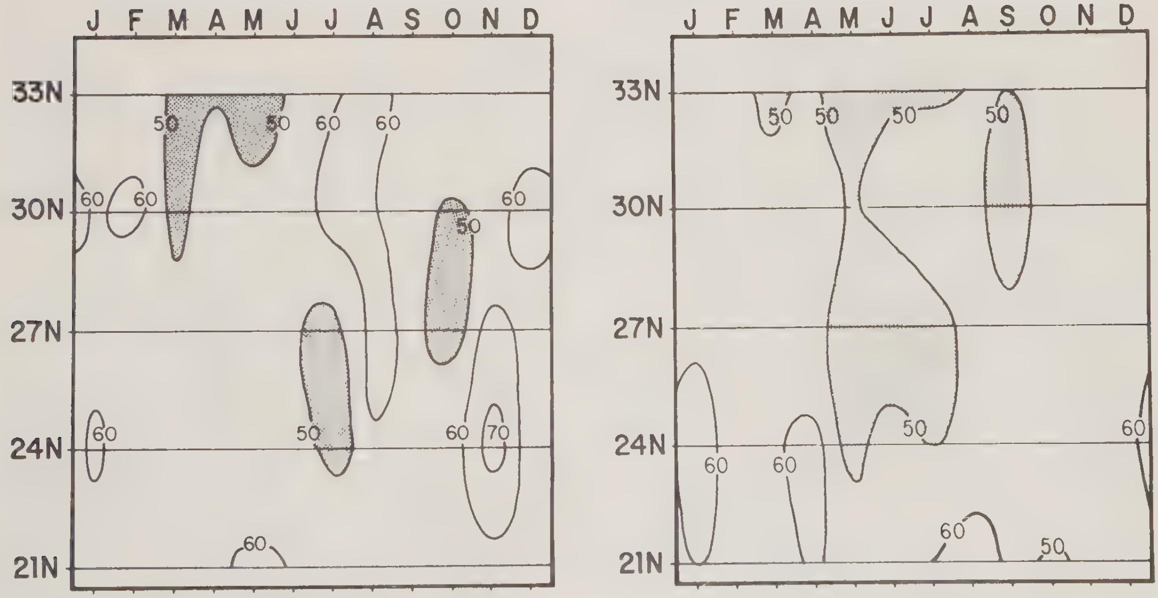
The daily anomaly has the same sign as the previous day's anomaly about 70 to 80% of the time depending on month and location (Figure 28A). By the second day (Figure 28B) the persistence of sign has dropped below 50%, indicating no tendency for persistence, at some months and locations. After 5 days, the months and locations where the anomaly is below 50% are considerably greater in number than those where it is greater than 60%. Thus any persistence of individual wind stress events on scales greater than 5 days appears to be slight.

In examining these series, however, one notices a certain persistence on longer scales which is evident in groupings of individual events resulting in general levels of average intensity above or below the seasonal norm. To illustrate this a similar analysis was performed on monthly anomalies. In order to have access to a longer data series for such a monthly analysis we have used a series computed from monthly mean pressure fields which extends back to 1946. Bakun (1973) has shown that indices computed in this manner correlate highly with corresponding series of monthly means of 6 hourly indices. In order to have a value 5 months previous to our first data point for comparison, we begin with June, 1946, and then work through the following 28 years ending May, 1974. The resulting distributions (Figure 29) are somewhat more noisy than those produced from the daily series (Figure 28) because there are only 28 data points for each month and location compared to the 200 or more data points per month and location in the 7 year daily series. A level of persistence of



A. 1 DAY EARLIER

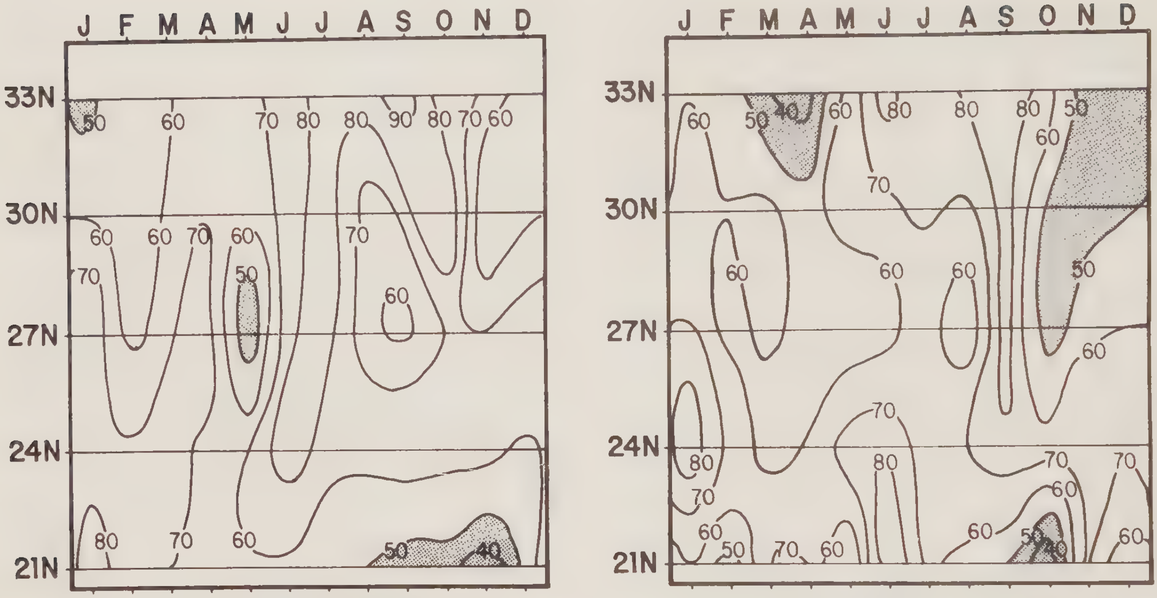
B. 2 DAYS EARLIER



C. 3 DAYS EARLIER

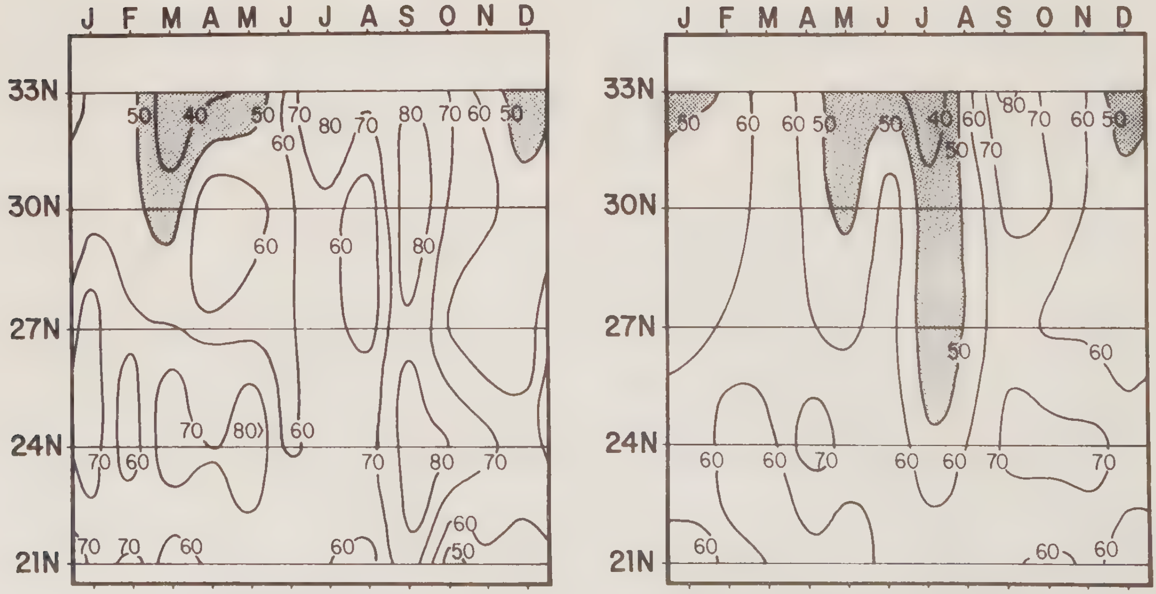
D. 5 DAYS EARLIER

FIGURE 28. Percentage of daily upwelling index anomalies having the same sign as the daily anomaly. A. 1 day earlier, B. 2 days earlier, C. 3 days earlier, D. 5 days earlier. A daily anomaly is defined as the difference between the daily average of 6 hourly coastal upwelling indices and the characteristic value for that day derived from the long term mean annual cycle. Period covered is 1967–73. Shading indicates percentages less than fifty.



A. 1 MONTH EARLIER

B. 2 MONTHS EARLIER



C. 3 MONTHS EARLIER

D. 5 MONTHS EARLIER

FIGURE 29. Percentage of monthly upwelling index anomalies having the same sign as the monthly anomaly, A. 1 month earlier, B. 2 months earlier, C. 3 months earlier, D. 5 months earlier. A monthly anomaly is defined as the difference between a monthly upwelling index value and a 20 year (1948–1967) mean value for the particular month. Period covered is June, 1946 through May, 1974. Shading indicates percentages less than fifty.

monthly anomalies after 5 months (Figure 29D) roughly equivalent to that for daily anomalies after 5 days (Figure 28D) is indicated.

One simple feedback system which may contribute to persistence of levels of upwelling intensity beyond the duration of individual upwelling events is as follows. An upwelling event or combination of events is eventually reflected in cooler water at the sea surface. This increases the temperature gradient in the lower atmosphere between the continent and the ocean, which in turn increases the onshore-offshore atmospheric pressure gradient. The result is greater longshore wind stress which feeds back to the upwelling process, transmitting an underlying level of intensity from one event to another. Whatever the major mechanism may be, these results suggest that general levels of upwelling intensity above or below the seasonal norm have a tendency to be persistent over periods approaching the seasonal time scale.

Spatial Coherence

Finally, an analysis using a spatial lag rather than a temporal lag, can yield some insight into the spatial coherence of upwelling anomalies. The percentage, by month and location, of daily anomalies having the same sign as the corresponding daily anomaly at 27°N latitude was determined (Figure 30). Again, we have required that the anomaly at 27°N be at least 10 $m^3/sec/100$ m of coast for it to be considered significant. The percentage at 27°N is of course always 100%. The percentage drops off more rapidly to the south than to the north. In fact at 21°N latitude it actually drops below 50% during September indicating the anomaly had a sign opposite to that at 27°N more often than not. In total, the indication is that coherence of upwelling anomalies over regions the size of the coast of Baja California is not necessarily to be expected.

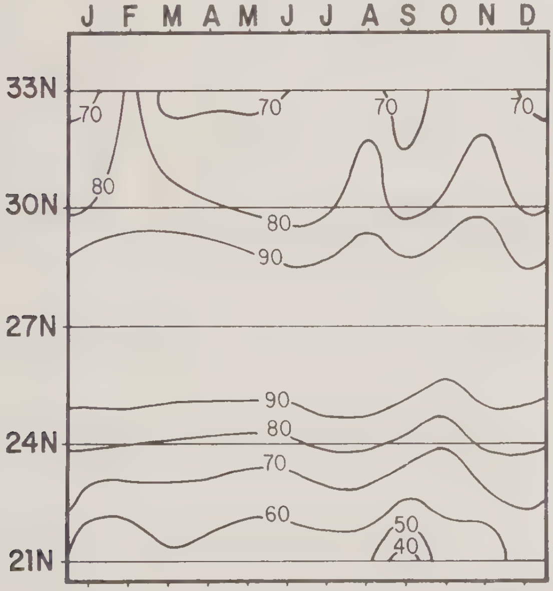


FIGURE 30. Percentage of daily upwelling index anomalies having the same sign as the corresponding daily anomaly at 27°N. Period covered is 1967–73. Shading indicates percentages less than fifty.

UPWELLING OFF BAJA CALIFORNIA DURING RECENT YEARS

We now attempt to characterize the upwelling situation off Baja California since 1972. Bakun (1973) presented coastal upwelling indices based on monthly mean data for the period 1946 through 1971. These are intended to represent the primary coastal divergence mechanism (Figure 2). These series were updated through July 1977 (Table 1) at 5 locations off southern California and northern Mexico (Figure 1). In computing these monthly indices a higher drag coefficient, 0.0026, was employed to roughly compensate for the underestimate of the stress caused by using mean data in the nonlinear calculation involved in equation (1).

In the section on the seasonal cycles we described the effect of the curl of the wind stress in causing convergence or divergence in the surface layer outside of the immediate coastal upwelling zone (Figure 19). This effect is probably important biologically. For example, certain organisms may be favored by a situation where the surface layer continues to diverge, on average, offshore of the coastal upwelling zone. Nutrients would continue to be fed into the surface layer, planktonic grazers swept away, etc. Other organisms may depend on concentration in convergent frontal zones of the organic material produced as a result of the upwelling near the coast. These might be favored by strong coastal upwelling in conjunction with or followed by strong offshore convergence.

In order to have an indicator of this effect, a set of indices of divergence of the Ekman transport field outside of the immediate coastal upwelling region was generated for the same locations and from the same monthly mean pressure fields as were the monthly coastal upwelling indices. The applicable equation is derived by Fofonoff (1963):

$$\nabla \cdot \vec{V}_E = \frac{1}{f}(\nabla \chi \vec{\tau}) \cdot \vec{k} - \frac{\beta}{f}\vec{V}_E \cdot \vec{j} \qquad (3)$$

where:

$\nabla \cdot \vec{V}_E$ represents the divergence of Ekman transport

$(\nabla \times \vec{\tau}) \cdot \chi$ represents the vertical component of the curl of the wind stress

f is the Coriolis parameter

β is the meridional derivative of f,

$\vec{V}_E \cdot \vec{j}$ is the meridional component of Ekman transport.

The stress and Ekman transport inputs to equation (3) were computed as for the monthly mean upwelling indices. Numerical values were assigned as vertical velocities required to balance the computed divergences (Table 2).

During the early months of 1972, coastal upwelling appears to have been generally stronger than normal (Figure 31). This was accompanied by anomalous offshore convergence except in the extreme south where anomalous offshore divergence tends to be a persistent feature (Figure 32). Late summer and early fall of 1972 are characterized by lower than normal coastal upwelling index values except during September in the southern portion of the region. The month of December shows stronger than normal upwelling index values along the whole coast. An anomalously divergent situation is indicated offshore during November and December.

TABLE 1

Monthly coastal upwelling indices *

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
					1972							
33N	8	33	168	228	243	283	254	201	144	36	16	24
30N	91	88	186	180	165	168	125	113	90	61	67	85
27N	120	138	199	236	197	162	101	58	94	64	77	81
24N	85	77	161	197	179	156	53	12	84	24	59	45
21N	86	86	128	117	74	97	5	-1	13	1	38	26
					1973							
33N	15	1	182	216	290	282	288	234	167	65	75	24
30N	65	7	178	193	155	178	137	149	121	90	93	97
27N	105	28	173	181	148	138	90	115	138	106	117	97
24N	68	34	155	142	142	107	55	83	122	84	106	72
21N	39	52	163	116	108	83	16	10	27	8	19	33
					1974							
33N	1	43	91	207	372	330	229	245	159	97	26	4
30N	22	104	93	234	284	263	147	167	141	104	74	34
27N	56	105	123	208	208	160	67	116	94	80	60	39
24N	52	78	100	138	147	82	24	50	53	54	43	57
20N	31	60	81	53	125	22	4	1	4	-1	5	37
					1975							
33N	10	45	123	197	282	362	322	251	166	100	55	16
30N	50	62	127	174	187	197	192	194	180	146	134	58
27N	43	84	127	183	165	161	99	115	117	133	99	40
24N	45	85	133	185	130	93	37	46	50	96	56	35
21N	19	47	41	75	100	28	2	-1	-8	6	28	26
					1976							
33N	-1	34	120	198	304	262	277	212	88	50	4	-6
30N	44	64	139	160	231	199	160	145	70	80	54	28
27N	27	51	127	158	215	214	142	170	57	58	28	17
24N	24	50	127	153	191	172	107	86	57	72	34	32
21N	21	33	122	125	119	36	30	4	1	16	18	35
					1977							
33N	9	57	163	207	224	325	285					
30N	38	131	201	169	182	222	181					
27N	10	110	189	206	224	252	135					
24N	23	96	153	194	184	163	79					
21N	83	92	230	192	260	134	70					

* Units are cubic meters per second per 100 m length of coast. Values signify volume transported offshore in the surface Ekman layer.

TABLE 2

Monthly Surface Layer Divergence Indices*

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
					1972							
33N	280	15	242	−195	−328	−465	−689	−155	−218	−31	204	211
30N	97	−326	−434	−627	−651	−801	−687	−458	−408	−154	96	76
27N	−240	−236	−584	−88	−217	−232	−157	−82	−168	42	−1	82
24N	−197	−126	−255	−167	−310	−112	−10	−43	3	−24	−19	5
21N	471	354	380	321	371	303	97	9	138	29	172	87
					1973							
33N	68	−9	267	100	−367	−130	−231	−73	−45	126	119	260
30N	−6	−23	−299	−461	−892	−924	−770	−652	−726	−338	−359	63
27N	−31	−63	−165	−186	−225	−220	−239	−157	−208	−52	−124	90
24N	27	−97	−181	−189	−265	−236	−177	−62	65	22	−23	12
21N	36	152	−43	32	88	163	1	119	133	90	155	195
					1974							
33N	25	375	−103	187	−387	−651	−334	−506	−81	−69	241	310
30N	−22	18	−338	−591	−969	−903	−590	−907	−556	−385	3	151
27N	−67	−49	−118	−136	−207	−135	−45	−112	61	114	116	−65
24N	−8	−81	−121	−103	−203	−131	33	−66	30	−23	−20	−138
21N	141	135	−43	103	25	126	7	−6	88	69	140	274
					1975							
33N	390	30	−9	−65	−387	−1116	−709	−651	−73	129	416	312
33N	189	−204	−332	−503	−909	−1223	−741	−832	−535	−379	46	71
27N	−10	−65	−106	−200	−256	−350	−309	−149	−28	−45	111	15
24N	−111	−127	−160	−91	−166	−163	−163	−88	−64	−94	−37	−40
21N	97	150	135	119	13	20	−13	8	91	131	245	186
					1976							
33N	393	206	376	−64	−201	−277	−350	−570	−30	123	246	230
30N	128	−52	−180	−643	−1097	−1021	−1009	−975	−345	−155	110	111
27N	25	−26	−192	−169	−227	−311	−332	−279	−40	71	142	41
24N	−93	−55	−144	−4	−155	210	−4	41	64	−64	−44	−83
21N	223	215	486	573	553	389	368	128	109	357	413	489
					1977							
33N	230	315	317	−111	−160	−827	−493					
30N	98	−12	−470	−787	−982	−1557	−1155					
27N	72	157	−75	−416	−449	−681	−269					
24N	−137	−5	−217	−409	−218	−131	−27					
21N	668	719	289	382	−312	95	228					

*Values signify vertical velocities at the bottom of the Ekman layer required to balance the indicated divergence or convergence occurring offshore of the primary coastal upwelling zone. Units are millimeters per day, positive upwards.

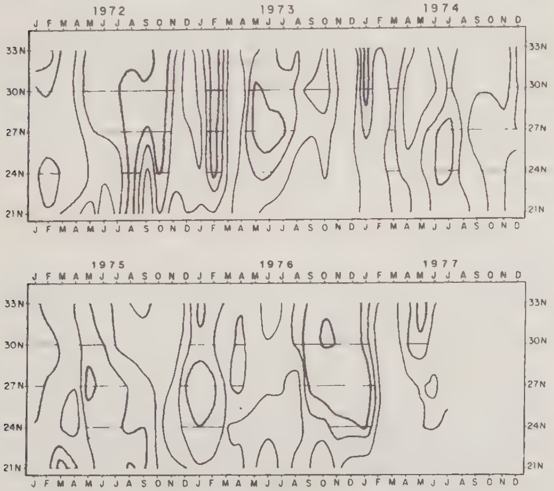


FIGURE 31. Monthly coastal upwelling index values (Table 1) in terms of quartiles of the frequency distribution made up of all values for the given location and calendar month within the 1946–77 time series. Quartiles are delineated by contours. The two quartiles below the median are shaded.

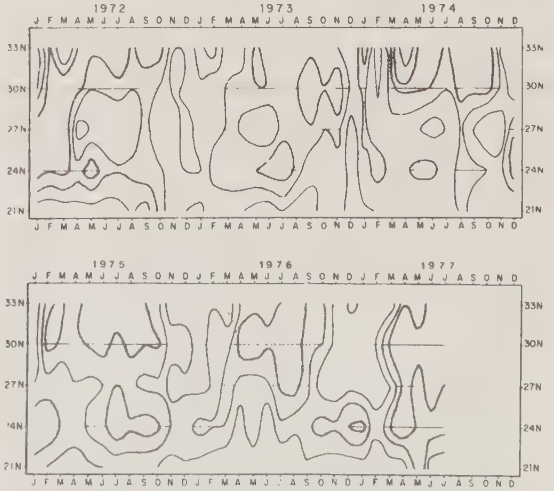


FIGURE 32. Monthly offshore surface layer divergence indices (Table 2) in terms of quartiles of the frequency distribution made up of all values for the given location and calendar month within the 1946–77 time series. Quartiles are delineated by contours. The two quartiles below the median are shaded.

Weak coastal upwelling is indicated off Baja California in February followed by higher than normal intensity during March and April (Figure 31). In the north a low tendency prevailed from May through October coupled with greater than normal offshore convergence. At 21°N latitude the coastal upwelling indices were anomalously high all year, becoming extremely anomalous late in the year. Extreme values appear all along the coast during November and December. The indication of high offshore divergence which is a persistent feature at 21°N during the recent period spreads northward along the whole coast during December (Figure 32).

An alternating pattern off northern Baja California was evident during early 1974 with a low upwelling index anomaly in January, a high anomaly in February, a low in March, and very high values in April and May. Low values appear in the south central region during June and July. The northern area is characterized by anomalous offshore convergence from May through October.

Generally higher than normal coastal upwelling is indicated during March 1975, followed by a period of lower than normal intensity which lasts until May in the north, but continues generally through the summer in the south. The latter portion of 1975 exhibits higher than normal coastal upwelling index values. The offshore region appears to have been anomalously convergent, particularly during summer and early fall (Figure 32).

A period of weak coastal upwelling is indicated during early 1976, followed by stronger than normal upwelling during the summer. The fall and winter are characterized by lower than normal upwelling index values as far south as 24°N latitude. The offshore divergence index values indicate anomalous convergence in the north during spring and summer of 1976, and anomalous divergence during late fall.

During the final revision of this paper, index values were available for the first 7 months of 1977. Coastal upwelling index values are generally above average except during January and during May in the north (Figure 31). Offshore divergence index values are high during January and February, but anomalously low during spring and early summer (Figure 32).

Offshore divergence index values at 21°N tend to be very high in this recent 6 year period relative to the values in earlier years of the time series (Figure 32). Whether this reflects a real longer period variation in the wind pattern is not clear at this time. Changes in the distribution of available data or in the meteorological analysis procedures may be affecting the computed values. In general, care should be exercised in attempting to discern long term trends using this type of index series. Rather, the purpose is to provide a useful indication of relative variations within groups of fairly contemporaneous years.

CONCLUDING REMARKS

In our descriptions of seasonal features, the summaries by 1 degree squares indicated significant spatial variations on scales smaller than the 3 degree resolution we can achieve in synoptic indices. Relating the large scale indices to smaller scale features may require the "engineering approach" suggested by Smith (1968) where one looks at the "outputs," in our case physical or biological data on a smaller scale in those particular instances where it is available from research cruises, shore stations; etc., and the larger scale synoptic "inputs" and attempts to define the "transfer functions." As a first approximation it may be reasonable to assume, for example, that where greater than normal convergence is indicated on the larger scale, smaller scale divergences which exist might weaken and convergences strengthen.

We are continuing to assemble pertinent data including ocean-atmosphere heat exchange components, dynamic topographies from hydrographic data, sea level records, mixed layer depths, temperature series from shore stations, river runoff records, etc. We are looking into possibilities of satellite inputs and are in the process of expanding our wind stress indices to lower latitudes using newly developed "global band" atmospheric products (Lewis and Grayson, 1972).

Our plans for the future include computer modelling of some of the processes controlling the fishery environment. It is sometimes the case in fishery oceanography that rather than having too little detail in our environmental descriptions we have too much, and very little means to integrate it into a total "environmental condition" which will make sense in terms of a total fishery. Modelling, rather than creating any new data, may help to distill the various data available down to a useable number of significant factors, the year to year variations of which could be quantitatively compared. Time series of these factors might be generated from historical data and related to the past history of fishery stocks. Continuous operational updates could than perhaps provide practical environmental inputs for systems approaches to fishery management.

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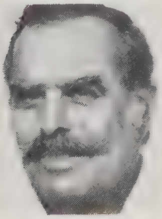
MFR PAPER 1246

Porpoise Rescue Methods in the Yellowfin Purse Seine Fishery and the Importance of Medina Panel Mesh Size

ERIC G. BARHAM, WARREN K. TAGUCHI, and STEPHEN B. REILLY

ABSTRACT—Introduction of the porpoise releasing method known as "backdown" by Anton Meizetich and Manuel Neves and the development of small-mesh porpoise safety panels by Harold Medina raises the question of the optimum mesh size for the panels. Medina panels of relatively standard dimensions hung from 2-inch mesh webbing had been installed in about half the nets of the U.S. tuna purse seine fleet before passage of the Marine Mammal Protection Act. The fishermen believed, and several statistical studies indicated, that use of the panel resulted in lower porpoise mortality. Despite the improved performance, however, porpoises were still being entangled in nets during the backdown process and a recent study indicates that up to 30 percent of porpoise mortality is due to this factor. Using mainly porpoise specimens taken in the fishery, measurements of penetration of porpoise snouts and flippers through mesh openings of 2, 1⅞, 1½, and 1 inches were made to elucidate the potential reduction in porpoise entanglement that could be expected through use of Medina panel mesh sizes of less than 2 inches. With their jaws closed, the snouts of even the smallest specimen could not penetrate 1-inch mesh, and the average penetration with the jaws open was grossly reduced as were penetrations of pectoral fins. Because of added weight and drag, additions of large sections of small-mesh netting can drastically affect the buoyancy and hydrodynamic performance of purse seines. Recent tests of porpoise "aprons" and "chutes" (trapezoidal-shaped sections of webbing appended to Medina panels) promise a means of making small-mesh netting compatible with tuna purse seine performance.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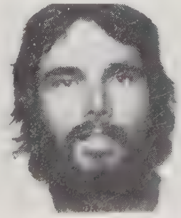
Reilly

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INTRODUCTION

Historically, fishermen have attempted to select netting of a mesh size that retains their target species while permitting unwanted species or sizes to escape. The situation in the eastern tropical Pacific U.S. tuna purse seine fishery, however, is complex. In this fishery the majority of the most important species, the yellowfin tuna, *Thunnus albacares,* is taken by scouting, herding, and setting purse seine nets on schools of porpoise with which the larger yellowfin associate (Perrin, 1968; Green et al., 1971). Three species of pelagic dolphins, or porpoise as they are more commonly referred to in the fishery, are primarily exploited by the fishermen. In order of decreasing importance, these species are: the spotted dolphin, *Stenella attenuata;* the spinner dolphin, *S. longirostris;* and the common dolphin, *Delphinus delphis.* In the fishery, these cetaceans are referred to respectively as spotters, spinners, and whitebellies. The races and distributions of the stocks are described by Perrin (1975) and Evans (1975).

When "porpoise fishing," as the method is called, the objective of the fishermen has been to retain the tuna and free the porpoise, but because the two forms are approximately the same size it is not possible to separate them by mesh-size choice. While capable of easily leaping over the corkline, porpoises show little tendency to escape in this manner. Thus, in the early years of the fishery, and despite the efforts of the fishermen, large numbers of porpoise were killed when they became entangled in the nylon webbing of nets or were sacked up with the tuna.

Because of the fishermen's subsequent development of a porpoise rescue procedure known as "backdown" and introduction of the related "Medina panel," mesh-size selection became an important consideration, and as a result of passage of the Marine Mammal Protection Act (Public Law 92-522, 92nd Congress, H. R. 10420, 21 October 1972), a consideration that has legal as well as practical implications. This law also mandated the National Marine Fisheries Service (NMFS) to work with the fishermen to develop porpoise-saving gear and methods. In the spring of 1973, research directed towards this objective began at the Southwest Fisheries Center in La Jolla, Calif., under the direction of Richard McNeely, who had studied tuna purse seining following the conversion from pole-and-line fishing (McNeely, 1961).

Several innovations such as hydraulic gates, skimmer nets, and various kinds of acoustic signals had previously been tried by Southwest Fisheries Center personnel. None had shown real promise. Therefore, in its early stages, the philosophy of the program was to work with the existing purse seining system and to help perfect those rescue procedures that the fishermen had developed, that they believed in, and that many of them were already using, to rapidly effect as great a reduction in porpoise mortality as possible. Progress in this work has previously been reported (Department of Commerce, 1974; Staff, Porpoise/Tuna Interaction Program, Oceanic Fisheries Resources Division, 1975 and 1976).

The objectives of this paper are to: 1) review the history of porpoise rescue procedures developed by the fishermen; 2) present measurements of the degree of penetration of porpoise appendages through various mesh sizes; and 3) to point out the importance of mesh-size selection.

MEDINA PANEL HISTORY

Prior to passage of the Marine Mammal Protection Act, fishermen experimented with methods and gear modifications that would reduce the incidental kill of porpoise. These efforts resulted in two related developments, "backdown" and the "Medina panel"

Backdown

Running a vessel in reverse to pull the corkline underwater to dump unwanted catches may have occasionally been used in the California sardine or mackerel purse seine fishery, but Anton Meizetich, captain of a small, San Pedro seiner, the original MV *Anthony M.*, is generally credited with developing this method of porpoise removal in 1959-60. Hearing of its success, Manuel Neves, captain of the MV *Constitution*, in 1961 demonstrated to his crew the effectiveness of the method in saving porpoise and time, and the use of backdown, as it came to be called, spread rapidly through the San Diego-based fleet which included the majority of the seiners that regularly fish on porpoise.

Various fishermen developed their own modifications of the method, but essentially, the process is executed by recovering about two-thirds of the net aboard the seiner, securing the hauling end and then, aided by the seine skiff functioning as a tug, moving the vessel in reverse in a wide arc. Coe and Sousa (1972) gave a detailed description of the methods used on one seiner in 1972. Pressure caused by pulling the netting through the water forms the net into a long channel approximately 90–110 m long and about 15–20 m wide (Fig. 1). As the backdown channel develops, porpoise tend to congregate at the extreme end or apex, while the tuna generally range back and forth in the channel between the porpoise and the seiner. At times when the tuna are near the seiner the vessel is backed rapidly, causing the corkline to submerge at the end of the channel where the porpoise are concentrated. The motion of the vessel continues to pull the corkline down and out from under the porpoise (Fig. 1). Usually, three or four such rapid backdown surges are necessary to spill the porpoise out of the net.

During the maneuver, the vessel's speed is crucial, for if backdown is too slow the porpoise may tend to swim with the net rather than passing over the submerged corkline. (This seems to be particularly true of spinner porpoise although behavior of the porpoises varies in different geographical locations.) Those porpoise that could not be backed out and that could be reached were hand-hauled over the corks by crewmen entering the water or working from a small skiff (cork tender). Porpoise were also removed from the net when concentrated with the fish in the bunt or bow end of the net at the time the captured tuna were landed.

Before and following passage of the Marine Mammal Protection Act, "skipper-gear workshops" were sponsored by the American Tunaboat Association in 1972, 1973, and 1974. At these meetings techniques were exchanged between fishing captains for refinement of the backdown process. During this period the stationing of the cork tender manned by one or two crewmen at the backdown area to pull up on the corkline whenever the loss of fish was threatened to aid porpoise over the corks, and to free porpoise entangled in the net became more widespread throughout the fleet (Fig. 1).

The Medina Panel

The second development, the Medina or safety panel, is closely related to backdown. In normal, trouble-free sets porpoise encircled by a purse seine usually loll at the surface, swim and dive in the open area of the net, and tend to avoid the corkline and the walls of webbing, but when porpoises are concentrated in the end of the backdown area and come in contact with the net, the potential for entanglement is greatly increased. Thus, despite the importance of backdown as a rescue technique, some animals are "gilled" in the net during the process and, unable to reach the surface to breath, they usually suffocate.

In the fall of 1970, tuna fishermen and scientists from the Southwest Fisheries Center met at the offices of the American Tunaboat Association to discuss porpoise rescue methods. Harold Medina, captain and owner of the MV *Kerri M.*, argued that strategically positioned smaller mesh would reduce the chances of porpoise entanglement. In December of that year while fitting out for the first trip of the 1971 season in Panama, Medina replaced the 4¼-inch (10.80-cm) stretch-mesh webbing in the top strip of his net in the backdown area with a section of 2-inch (5.08-cm) stretch-mesh webbing 720 feet long by 33 feet deep (about 219.5 by 10 m).

A brief parenthetic discussion of netting may be helpful at this point. Net webbing is measured from the center of one knot to the center of an adjacent knot while the webbing is stretched. Originally, tuna purse seines were hung with 4⅛-inch (10.5-cm) stretch mesh, but in recent years 4¼-inch (10.8-cm) mesh has become standard. The webbing is made from different types and sizes of twine spun from various synthetic fibers. Therefore, mesh dimensions are not critically standardized. Further, once in use, the

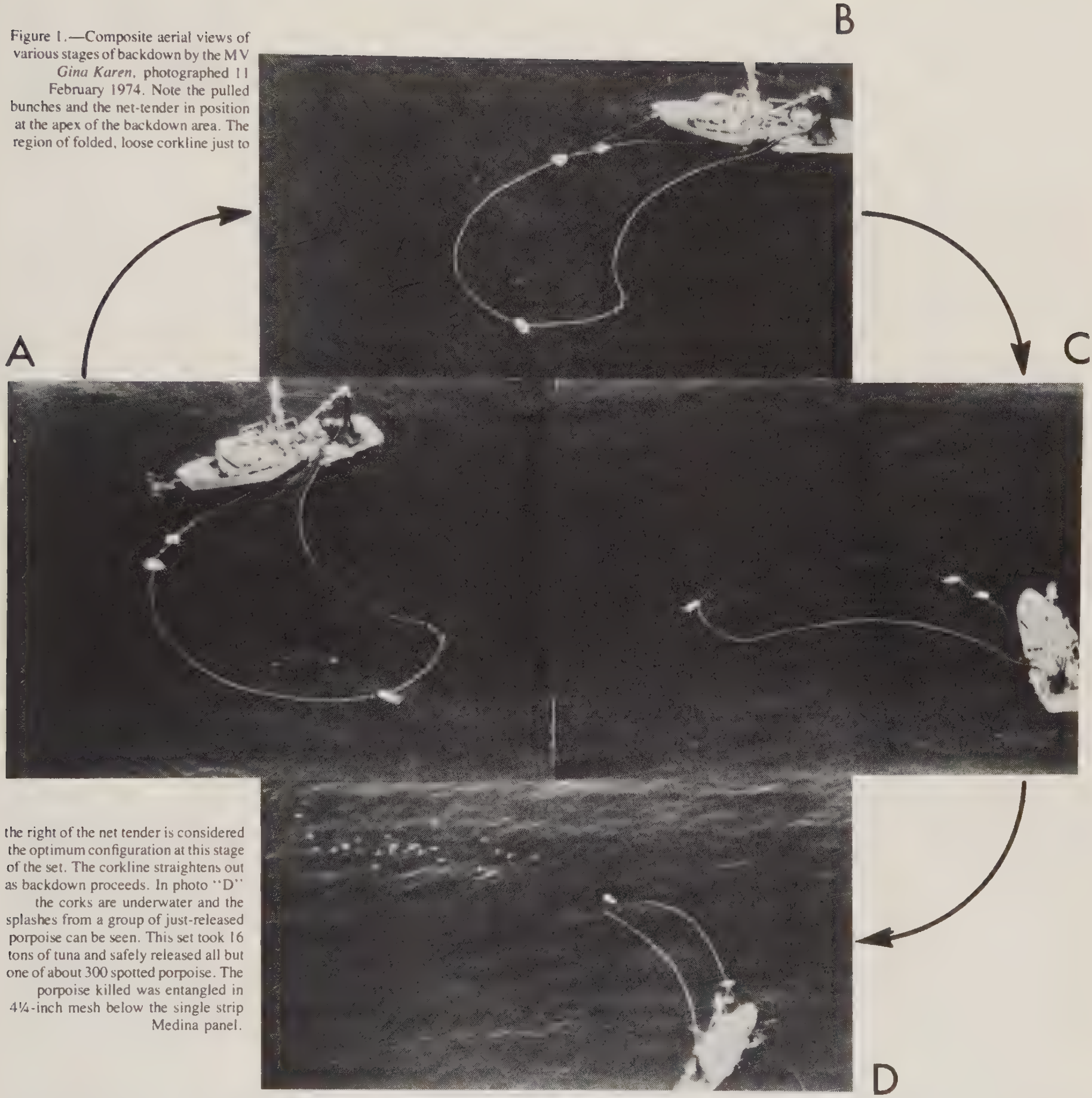


Figure 1.—Composite aerial views of various stages of backdown by the MV *Gina Karen*, photographed 11 February 1974. Note the pulled bunches and the net-tender in position at the apex of the backdown area. The region of folded, loose corkline just to the right of the net tender is considered the optimum configuration at this stage of the set. The corkline straightens out as backdown proceeds. In photo "D" the corks are underwater and the splashes from a group of just-released porpoise can be seen. This set took 16 tons of tuna and safely released all but one of about 300 spotted porpoise. The porpoise killed was entangled in 4¼-inch mesh below the single strip Medina panel.

mesh openings do not retain their original size but become smaller as the twine shrinks. As a general rule, webbing shrinks about 5 percent a year for the first 2 years it is used and then tends to stabilize. Purse seines are constructed by lacing together long strips of webbing that are about 120 fm (about 219.5 m) in length and usually 100 meshes deep (about 5.5 fm, or about 10 m). Thus, one strip of 4¼-inch mesh that has undergone shrinkage can conveniently be replaced by two strips of 2-inch mesh, each 112.5 meshes deep.

Later in the 1971 season a section of webbing similar to that used by Harold Medina was employed by his cousin, Joseph Medina, Jr., on cruises of the MV *Queen Mary*. These highly experienced and skilled skippers concluded that the smaller mesh in the backdown area was effective in reducing porpoise entanglements and did not degrade the performance of their nets. Harold Medina made available diagrams and instructions of panel installation and strongly recommended its use to other fishermen. By the end of the 1972 fishing season similar panels had been installed in the nets of approximately 40 to 50 percent of U.S. tuna seiners. Further voluntary adoptions raised the percentage of the fleet's nets equipped with such a panel to about 60 to 70 percent by the end of 1973.

While there was a general standardization of panel dimensions, each vessel operator experimented on the exact placement of the panel working out what he believed to be the most effective arrangement for his boat and fishing techniques.

Of primary importance to the fishermen in any net modification is its effect on what can be called "net control", that is, the ease and rate which the backdown area can be submerged to facilitate passage of the mammals over the corkline and out of the net at the opportune time while still being able to obtain a rapid rise of the corks to the surface to retain fish that may swim into the backdown area seeking escape. Aside from the buoyancy of the net and the skill and judgment of the captain and crew, such factors as the displacement, weight, and movement of the vessel, its power capabilities, responsiveness to the throttle, turning radius, availability of a bow thruster, and the towing, rigging, and operational characteristics of the seine skiff affect net handling. The tendency of webbing to foul with jellyfishes and other organisms and the vagaries of wind and sea can be added to these factors.

Most fishermen and industry spokesmen were convinced of the effectiveness of the Medina Panel. With some qualifications, four statistical studies completed between 1972 and 1974 on steadily increasing amounts of data obtained by NMFS observers during commercial fishing cruises (and with increasing sophistication) have reached the same conclusion (NOAA Tuna-Porpoise Committee, 1972; Stauffer, 1974; Norris and Dohl, 1974; Fabrick and Faverty, 1974). Several factors complicated the statistical analyses. The early data were sparse and obtained on vessels whose owners and skippers voluntarily accommodated NMFS observers rather than on randomly selected seiners. Thus, the results may not have been representative of fleet performance (placement of observers on randomly selected vessels was initiated in 1974). More importantly, the majority of the porpoise kill on any given trip occurs in a small percentage of the sets, usually where a problem has developed to hinder or slow the procedures. These problems frequently develop when a set has been made on either or both a large number of porpoise and a large tonnage of yellowfin tuna. In some cases the net has collapsed, that is the corklines have come together restricting the amount of open surface area, or large pockets or canopies have developed entrapping the porpoise in webbing before the operation has progressed to the backdown phase of the set. In such cases, obviously, it is difficult to fairly evaluate the reduced entangling factor of small mesh in the backdown area.

NMFS GEAR PROGRAM

Despite the improved performance of Medina panel-equipped nets over those which lacked the smaller mesh sections, underwater observations by NMFS gear specialists during charter cruises in 1972 and the records of porpoise observers from commercial fishing trips indicated that some porpoises were still entangling in nets during backdown. The animals were ensnarling in both the 2-inch web of the Medina panel and below or to the sides of the panel in the 4¼-inch mesh. Clearly, tests of more extensive panels hung with webbing of smaller than 2-inch mesh were strongly indicated.

Experimental Net

Following modeling studies, in the spring of 1973 an experimental purse seine was designed and built. The objectives of the design were to provide a large volume of water to safely contain large numbers of porpoise within a fully pursed net and at the same time create a deep, rapid-sinking net that would be advantageous on school fish sets that do not involve porpoise. Construction of the net also provided an opportunity to experiment with the Medina panel.

Although a few fishermen had used 1⅞-inch (4.45-cm) mesh knotless webbing, the standard Medina panels installed in the fleet's nets had mainly been hung with the equivalent of one strip of 2-inch stretch-mesh knotted webbing. There are several cogent reasons for using this dimension mesh: it is regularly hung in the large dip nets or brailers used to scoop tuna out of the sacked-up bunt end of the purse seine, and is therefore usually available; the 4¼-inch webbing shrinks to approximately 4 inches after moderate usage and the 2-inch mesh can be easily laced in, two meshes to one; and even though the small mesh will suffer shrinkage after use, the lines of strain work well in the net with the larger mesh.

The Medina panel of the experimental net was constructed from 1½-inch (5.08-mm) stretch-mesh webbing that is generally used for shrimp trawls. This webbing was extended in depth to the equivalent of three strips deep (about 30.2 m), so that the small mesh extended down to reach the floor of the channel where porpoise frequently dive during backdown. The panel was also extended in length to reach from the stern tie-down point through the third bunch which is generally gathered along side the bow of the vessel at backdown (see Fig. 1). This design would then afford the porpoises protection from large mesh around the entire periphery of the backdown channel. Lighter-than-normal thread used in the 1½-inch mesh webbing tended to compensate for the added drag caused by the increased amount of small netting.

Early tests of the net during the fall of 1973 on the cruise of the MV *John F. Kennedy* indicated some defects, but a highly encouraging low kill rate was achieved. Both the NMFS gear specialist aboard, Jerry Jurkovich, and the captain, Lionel Souza, credited the more extensive, small-mesh Medina panel with much of the success. Only one porpoise was noted entangled in the small mesh, and that was where the 1½-inch mesh had been torn. Distracting to some extent from the success of this trip was the fact that it was a research charter that granted fishing rights for yellowfin tuna inside the Inter-American Tropical Tuna Commission Yellowfin Regulatory Area (CYRA) and therefore was not typical of the more competitive fishing that prevails earlier in the year during the open season.

In June 1974, a captain of a new seiner volunteered to further test the net and to carry Jerry Jurkovich. The trip was made to the area west of the CYRA where the vast majority of the fishing is on porpoise and conducted under rigorous weather and sea conditions. This cruise achieved what was at that time a record low kill-rate. The small-mesh Medina panel again was considered by Jurkovich of major importance in this performance.

Small Mesh Considerations

Based on these successful, although limited tests of the more extensive smaller mesh Medina panel and the common sense principle that tapered objects, such as porpoise snouts and fins, will not penetrate as deeply into small openings as they will into larger openings, it would seem that the more extensive smaller mesh panels would have been rapidly introduced into the fleet. However, in the real world of tuna fishing other considerations are operative as well.

Purse seines in the modern tuna fleet tend to be tailored to the size of the vessel that will deploy them and to a lesser extent to the type of fishing that will mainly be conducted. Basically, there are three types of fishing: porpoise fishing, log fishing, and school fishing. In the latter cases, schools of tuna that are not associated with porpoises are located and entrapped. The larger vessels use the larger nets and school fishing nets are generally about 100 fm longer than porpoise fishing nets. Most of the newer vessels fishing on porpoise now use nets 600–700 fm (1,097–1,280 m) in length and 10–14 strips deep (about 101–141 m). Because of its added weight, drag, and tendency to clog, addition of large amounts of small-mesh webbing to a net of this size must be approached with caution, for the buoyancy of the net can be lessened to the point that once the corks go under and are squeezed by increasing water pressure they will not rise to the surface. In such a situation, the net can sink to the point where it and even the vessel are in jeopardy.

Again, what appears to be a simple matter of mesh-size opening is complicated by numerous factors. For example, the stretch of the webbing at any given moment can close the area of the openings both before or after penetration of the animal appendage. The angle of incidence of the animal appendage in relation to the plane of the webbing, the dimensions and shape of the teeth or roughness of the skin that would tend to catch and hang in the thread, and the behavior of the animal which in turn may be affected by many variables, are other imponderables that are difficult to predict.

Live Animal Experiments

In view of the above discussed considerations, the most valid tests of mesh-size entanglement factors should be made on live animals under experimental conditions. Such experiments were planned for the summer of 1973 as part of the behavioral studies undertaken for NMFS by the University of California, Santa Cruz, Calif. (Norris and Dohl, 1974). The problems of obtaining and maintaining live specimens of those stocks utilized in the fishery were insurmountable. Thus the Hawaiian spotted dolphin or ''kiko'', a race of *Stenella attenuata*, was chosen for the experiments. Unfortunately, the animals did not do well in the only cages available for use at the U.S. Navy Undersea Laboratory Marine Mammal Facility at Kaneohe Bay, Oahu, Hawaii. Of the eight animals captured and placed under husbandry, seven died. Because of the inherent dangers of the experiment, the remaining animal was only used in a series of trials of passage through net openings of various sizes similar to the experiments of Perrin and Hunter (1972). As an aside, it should be noted that this animal survived the tests and was released in the general area of his capture.

A casual observation made by Dohl (pers. commun.), but not included in the above cited report, is also of interest here. In all observed cases, when a porpoise had pushed its rostrum and lower jaw through a hole in their wire mesh enclosures, the animals kept swimming and forcing themselves further into the opening until they became exhausted and died. The animals never attempted to withdraw from the ensnaring hole. This behavior also seems to be typical of porpoises entangled in tuna nets. As the fishermen say, ''porpoise have no reverse gear.''

Table 1.—Relative life stages and measurements (in centimeters) of porpoise specimens used in the appendage penetration tests.

Specimens		Total length	Rostral length	Jaw ×-section closed		Jaw ×-section open				Pectoral fin length
						Upper		Lower		
Numbers	Description			Width	Depth	Width	Depth	Width	Depth	
1 (WFP 281)	Spinner, large adult female	185.0	13.7	3.3	3.5	3.4	1.8	3.2	2.0	23.5
2 (GMA 115)	Spinner, large juvenile female	127.5	11.3	3.1	3.4	3.1	1.5	3.2	2.1	20.1
3 (WFP 285)	Spinner, medium juvenile male	115.0	8.5	—	—	—	—	—	—	—
4 (WFP 290)	Spotter, medium adult female	182.0	11.0	3.3	3.6	3.3	2.1	2.6	2.0	—
5 (WFP 467)	Spotter, large juvenile female	144.0	9.4	3.2	3.6	3.2	1.5	2.5	2.1	—
6 (WFP 468)	Spotter, small juvenile male	87.0	5.5	2.6	3.0	2.6	1.6	2.5	1.4	14.5
7 (NUC 385)	Whitebelly, large juvenile female	146.0	11.6	4.2	4.0	4.0	2.3	3.9	2.6	24.2

PORPOISE APPENDAGE PENETRATION TESTS

Unable to acquire data obtained with live animals, we then carried out the tests described below on dead specimens to quantify the relative potential entanglement factor of various mesh sizes. The tests were done in April 1974 at the Southwest Fisheries Center.

Specimens

Seven animals representing the three porpoise species of major importance were used in the tests: three spinner dolphins, *Stenella longirostris;* three spotted dolphins, *S. attenuata;* and one common or whitebelly dolphin, *Delphinus delphis*. The specimens of the first two species were collected in the eastern tropical Pacific by NMFS observers on commercial fishing vessels and are representative of porpoises utilized in the fishery. The *Delphinus* was taken dead from a Baja California, Mexico, beach by Navy Undersea Center personnel and was probably from a stock that is not involved in the fishery (Evans, 1976). All specimens had been frozen and were thoroughly thawed before the tests were performed. To the extent possible, representative size classes were selected for measurement. Their sex and relative life stage is indicated in Table 1. In the cases of three specimens, number 3 spinner and numbers 4 and 5 spotters, only the heads had been collected and pectoral fin measurements and tests could not be made. The number 3 spinner specimen was damaged to the degree that critical cross sectional measurements were impossible. The nature of the longitudinal measurements made on specimens is indicated in Figure 2, and the pertinent dimensions are listed in Table 1.

Netting

Four different stretch-mesh sizes of coal-tar treated nylon netting were used: 1-inch, No. 18 thread; 1½-inch, No. 18 thread; 1⅞-inch, No. 54 thread (commercially known as 2-inch knotless); and 2-inch, No. 36 thread. (The metric equivalents for mesh sizes are shown in Figure 3.) The thread sizes indicate the number of yarns used for a strand and are not standardized diameters. The 1½-inch mesh webbing was a remnant of the panel built into the experimental net; the 1⅞-inch monofilament mesh was obtained from a commercial source and was not on hand at the time that specimen number 1 was run. The 1- and 2-inch mesh webbing was unavailable commercially at the time of the study and was hand-made by

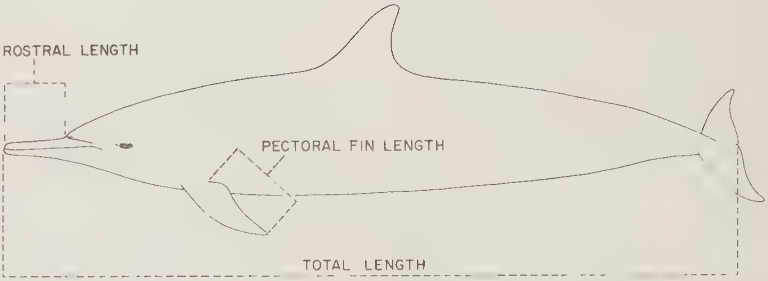
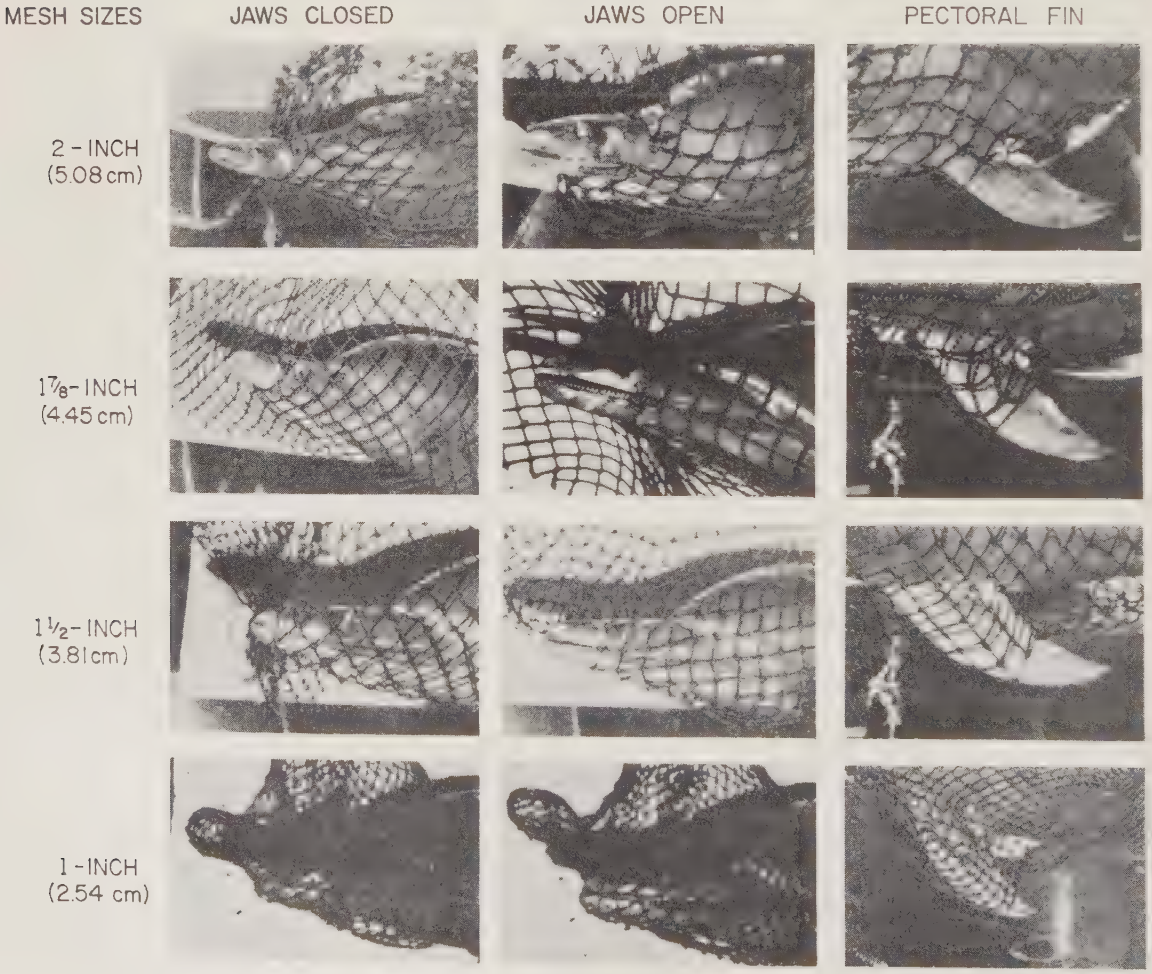

ROSTRAL LENGTH
PECTORAL FIN LENGTH
TOTAL LENGTH

Figure 2. –Longitudinal meaurements made on porpoise specimens used in appendage penetration tests.

Figure 3. —Photographs of penetration tests performed on specimen number 2, a relatively large juvenile female spinner porpoise. (Total length, 127.5 cm; rostral length, 11.3 cm; pectoral fin length, 20.1 cm.)


MESH SIZES
JAWS CLOSED
JAWS OPEN
PECTORAL FIN
2 - INCH
(5.08 cm)
1⅞- INCH
(4.45 cm)
1½- INCH
(3.81 cm)
1 - INCH
(2.54 cm)

a professional net builder. All the netting was new and had not been subjected to wear, stretch, or shrinkage.

Method

The netting was snugly pulled down over the rostrum or snout, first with the jaws tightly closed and then repeated with the jaws slightly agape. In the latter case, a net bar was inserted in the mouth and the mandible would penetrate one mesh opening and the lower jaw an adjacent mesh opening. Measurements of penetrations were made with a caliper from the tip of the upper jaw to the net twine. These measurements were then compared to the full-length of the rostrum (measured from the tip of the upper jaw to the apex of the melon) to derive the percent penetration of that specimen. Penetration of the pectoral fin, or "flipper," was similarly measured for the four entire specimens that were available. Measurements were rounded to a millimeter.

Results

Representative photographs of the tests are shown in Figure 4. The appendage penetration measurements through the four mesh-size openings for the three classes of tests, "jaws closed," "jaws open," and "pectoral fin," are listed in Table 2. The percent penetrations (depth of penetration/length of appendage × 100) are also listed and averaged in Table 2, and these average ratios are graphed in Figure 4.

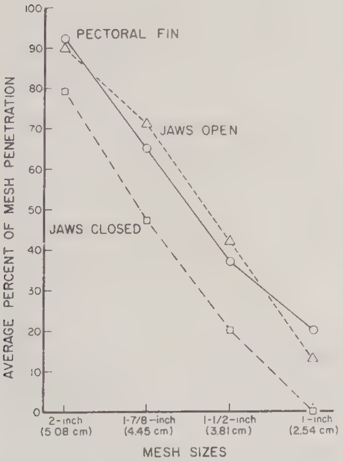


Figure 4.—Average ratios of percent penetration of porpoise appendages through the indicated mesh sizes.

The measurements demonstrate a direct relationship between the depth of penetration and mesh size, and the decreases are approximately linear and about the same rate for all three classes of tests (Fig. 3). Comparing the results for 2-inch and 1½-inch meshes, a marked decrease in penetration was measured for the smaller mesh. With the jaws closed the decrease was 75 percent; with the jaws open when two openings are involved, 53 percent; and the flipper penetration was reduced 60 percent. Surprisingly, the 1⅞-inch mesh (2-inch knotless), a coarse filament nylon net, also proved considerably lower than the 2-inch mesh. This was apparently due to the larger and coarser twine used in the netting. This twine was also more abrasive to the animal's skin than that of the other netting. Finally, the 1-inch mesh by far allowed the least penetration. With the jaws closed there was no penetration for any specimen tested (a reduction of 100 percent from the 2-inch average). With the jaws open, the average penetration was limited to only 13 percent, 86 percent less than the 2-inch measurement and also a marked reduction over the 1½-inch mesh.

Pectoral fin penetration of the four available specimens was restricted to only 20 percent, a decrease of 78 percent over that for the largest mesh.

Table 2.—Porpoise appendage penetration measurements (in centimeters), and the percent of penetration relative to the length of the appendage for four sizes of net mesh openings.

	2-inch mesh		⅞-inch mesh		1½-inch mesh		1-inch mesh	
Test specimens	cm	%	cm	%	cm	%	cm	%
Jaws closed								
1 Spinner, large adult female	9.0	66	—	—	1.5	11	0.0	0
2 Spinner, large juvenile female	9.4	83	4.9	43	2.3	20	0.0	0
3 Spinner, medium juvenile male	8.5	100	3.4	40	1.8	21	0.0	0
4 Spotter, medium adult female	8.3	75	3.7	34	1.3	12	0.0	0
5 Spotter, large juvenile female	7.3	78	4.2	45	1.9	20	0.0	0
6 Spotter, small juvenile male	5.5	100	5.5	100	2.6	47	0.0	0
7 Whitebelly, large juvenile male	5.8	50	2.5	22	1.1	9	0.0	0
Average % penetration		79		47		20		0
Reduction from 2-inch				41		75		100
Jaws open								
1 Spinner, large adult female	10.5	77	—	—	2.6	19	1.1	8
2 Spinner, large juvenile female	10.8	96	6.6	58	4.2	37	1.1	10
3 Spinner, medium juvenile male	8.5	100	8.5	100	4.3	51	1.6	19
4 Spotter, medium adult female	11.0	100	6.9	63	3.6	33	1.1	10
5 Spotter, large juvenile female	9.3	100	5.8	62	4.3	46	1.8	19
6 Spotter, small juvenile male	5.5	100	5.5	100	4.4	80	1.5	27
7 Whitebelly, large juvenile male	6.8	59	5.1	44	3.0	26	0.0	0
Average % penetration		90		71		42		13
Reduction from 2-inch				21		53		86
Pectoral fin								
1 Spinner, large adult female	16.4	70	—	—	10.9	46	6.1	26
2 Spinner large juvenile female	20.1	100	10.7	53	7.5	37	3.7	18
3 Spinner, medium juvenile male	—	—	—	—	—	—	—	—
4 Spotter, medium adult female	—	—	—	—	—	—	—	—
5 Spotter, large juvenile female	—	—	—	—	—	—	—	—
6 Spotter, small juvenile male	14.5	100	14.5	100	5.8	40	3.1	21
7 Whitebelly, large juvenile male	24.2	100	10.3	43	5.7	24	3.4	14
Average % penetration		92		65		37		20
Reduction from 2-inch				29		60		78

Discussion

The most recent analysis of data taken by NMFS observers on causes of porpoise mortality during commercial fishing trips indicate that over a 2-year period the kill caused by entanglement varies from about 28 to 55 percent depending on the species (Staff, Porpoise/Tuna Interaction Program, Oceanic Fisheries Resources Division, 1976). The rostrum is the most common appendage involved in entanglement, and the numerous, small, conical teeth frequently catch in the twine and play an important part in entanglement. Occasionally, having first become entangled by the rostrum or the jaws the porpoise roll and thrash becoming further entangled by other appendages.

Regarding the penetration test results, while reduction of penetration of porpoise rostra with smaller mesh sizes would logically be expected, the drastic limitation of penetration resulting from a 1-inch decrease in mesh size was striking. It should be noted, however, that even the 1-inch mesh would not totally exclude the tip of the jaws when they were agape. Clearly, however, the test results strongly indicate the potential reduction in entanglement that can be gained through the application of small-mesh netting.

RECENT DEVELOPMENTS

MV *South Pacific* Charter, 1974

As previously indicated, in the past the hesitancy of some fishermen to adopt smaller-mesh Medina panels has been based on their well-founded apprehension about the weight and drag effects of decreased mesh size that can grossly affect the hydrodynamic performance of the net. However, a relatively recent development, the "porpoise apron" may offer one solution to this problem. Designed by Richard McNeely and first tested on the NMFS charter cruise of the MV *South Pacific* in the fall of 1974, the apron is a tapered, trapezoidal section of small-mesh webbing. The apron is centered at the middle of the backdown area and the webbing section is laced in between the corkline and the Medina panel.

Because of the apron's tapered sides, the amount of webbing between the cork and chain lines at the apex of the backdown area is now longer than at the sides. This transfers the strain on the webbing from the center of the backdown area to its margins when the net is in backdown configuration. Several desirable effects result. The deep, porpoise entrapping pocket that commonly forms under the corks at the end of the backdown area tends to be eliminated. Instead, the panel and apron form a ramp that eases the porpoise over the corkline during backdown. It is therefore unnecessary to sink the corks to considerable depths with strong backdown surges, but rather a slow continuous backdown can be performed.

The *South Pacific* charter staged in Panama City, Panama, and the prototype apron was hung with locally available 2-inch mesh webbing when the intended 1¼-inch webbing was lost in air transit. The *South Pacific* charter results were highly encouraging, and the apron was left in that vessel's net for the 1975 season.

During the *South Pacific* charter, McNeely also briefly experimented with an extension to the apron called a "chute". This severely tapered, trapezoidal-shaped section of netting was hung from untarred, 1¼-inch mesh borrowed at sea from another purse seiner under charter to NMFS. From the deck of the *South Pacific* during backdown, the dark bodies of porpoise could easily be seen in contact with this light-colored webbing. The porpoise would come free without entangling. The ship's fishing captain, Joseph Scafidi, was highly impressed with the performance of the small-mesh webbing. For the 1975 season, Scafidi transferred to another seiner and he requested and received from NMFS 1¼-inch mesh webbing for testing from which he hung an apron in the net of his new vessel.

Concurrent with the *South Pacific* charter, another charter vessel, the *J. M. Martinac*, was fishing with a net that had a 120 fm Medina panel of 1¼-inch webbing. The NMFS gear technician, Daniel Twohig, also observed a striking lack of entanglement during contact with this small-mesh Medina panel.

Voluntary April Tests, 1975

In mid-spring of 1975, a group of fishermen who had returned to San Diego following their first trips of the season met with owners and managers to discuss porpoise rescue procedures. Joseph Scafidi attended and he strongly recommended small-mesh panels and aprons. August Felando, General Manager of the American Tunaboat Association, asked for volunteers, and eight captains or managers agreed to install and test aprons during the remainder of that season.

Unfortunately, this period coincided with a world shortage of synthetic-fiber twine due to the petroleum shortage and the destruction by fire of a major twine producer's factory. Orders could only be filled after at least a 6-month delay. The vessels of the "apron volunteers" were in port for only brief periods between fishing trips, and, as a result, most of these aprons were hung with the only small-mesh netting locally available, 2-inch stretch mesh, woven from coarse nylon.

One of us (E. G. Barham) interviewed the "apron skippers" on their return from their first fishing trip with the aprons. In general, their opinions were affirmative, although some troubles were reported due mainly to aprons that were not precisely centered in the backdown area.

MV *Bold Contender* Charter, 1975

Small-mesh modifications designed by McNeely were further tested in the fall of 1975 on the charter cruise of the MV *Bold Contender* under command of John Gonsalves. Operating from a small rubber-raft using face mask and snorkle, James Coe of the Southwest Fisheries Center observed the behavior of the animals and the net in the backdown area. Coe discovered that many animals thought to be laying dead at the bottom of the net were actually alive, and if enough time were allowed, these animals would surface for air and could be safely released. Coe would signal the captain when all live porpoise were out of the net and backdown could be ended. The net for these tests was hung with a double strip (11 fm deep) Medina panel, and a longer apron with a chute laced to its distal margin. All small-mesh webbing was 1¼-inch stretch mesh. This configuration developed a longer, gently inclined ramp in the region where the porpoises concentrated, and during backdown the decreased straining area of the small mesh created an increased flow of water that helped to "wash" the porpoises over the corkline. At the same time, a

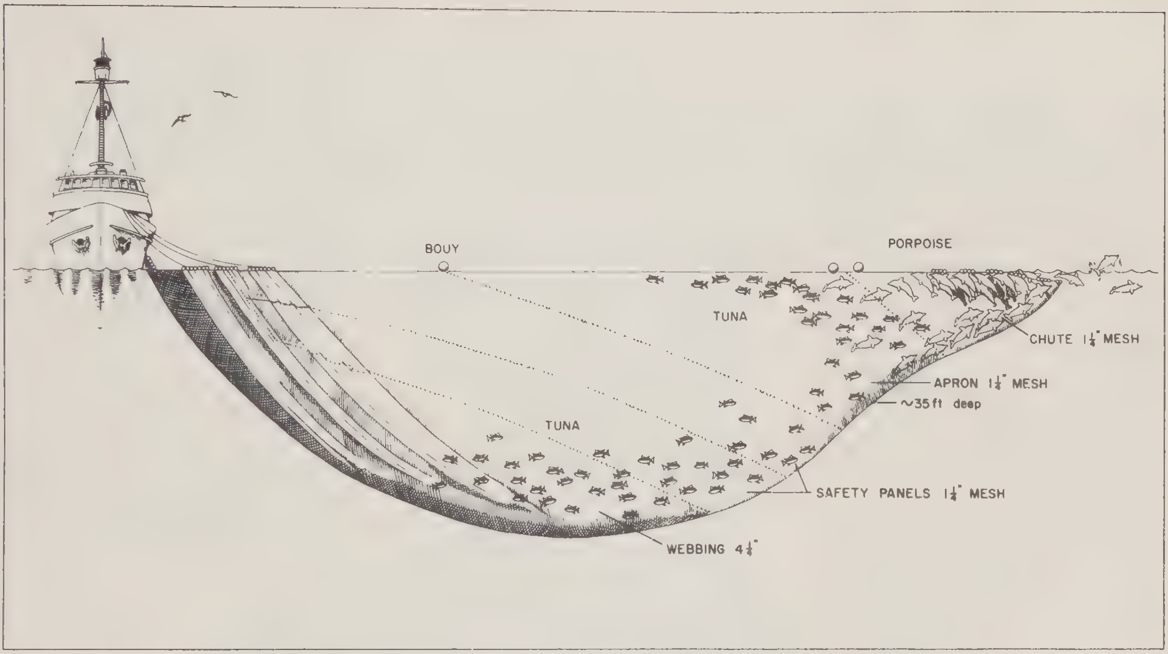


Figure 5.—Schematic cross-section of the apron-chute, double Medina panel, configuration in a tuna purse seine during backdown. Mesh sizes of the various components are indicated.

deep pocket was formed in an area in front of the Medina panel that tended to hold the tuna away from the backdown area (Fig. 5). This arrangement of small-mesh netting in conjunction with other devices and methods is now known as the "Bold Contender System" (Staff, Porpoise/Tuna Interaction Program, Oceanic Fisheries Resources Division, 1976). An extremely low porpoise mortality was recorded during this charter cruise.

Major Field Tests, 1976

There was some doubt as to whether the success of the *Bold Contender* charter was mainly due to the apron and chute, to the extensive small-mesh Medina panel, or to the observer in the small rubber raft. However, as a result of these tests, NMFS and the newly formed tuna industry sponsored Porpoise Rescue Foundation inaugurated a major testing and evaluation program in 1976. As planned, 10 vessels would fish with a double-strip Medina panel and an apron and chute all hung from 1¼-inch stretch-mesh webbing, and another 10 seiners would fish with only a double strip, 1¼-inch Medina panel. Both sets of vessels were to use a face-mask equipped observer working from a small rubber raft. The vessels would also use the other aspects of the Bold Contender System and NMFS field technicians would accompany all vessels and record performance.

As the 1976 season progressed, some of the test trips were aborted due to Judge Charles Richey's court ruling on the validity of the permit to take porpoises issued by NMFS to the American Tunaboat Association, but at this writing most of these trips have been resumed and data are rapidly accumulating from approximately the full vessel complement.

Regardless of the final outcome relative to the apron and chute vs. the extended 1¼-inch Medina panels, it appears that the introduction of small-mesh netting will make a major contribution to further reductions of incidental porpoise mortality in tuna purse seines[1].

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[1] While this manuscript was in review, preliminary results of the MV *Elizabeth C. J.* 1976 charter cruise became available. To obtain the cooperation of this modern seiner it was necessary to combine yellowfin tuna allotments for both gear work and behavioral research. The gear work was essentially a continuation of the "Bold Contender System" approach, and the net was equipped with an extensive Medina panel and modified apron hung from 1¼-inch mesh webbing. The results were extremely successful. During the cruise the *Elizabeth C. J.* made 45 sets on porpoise which took 917 tons of yellowfin tuna with only 15 porpoise being killed. Further, the majority of these animals were killed as a result of the behavioral research objectives rather than normal fishing operations. This record low kill rate was attributed to four factors: 1) a successful culmination of NMFS gear research under the direction of Richard McNeely; 2) the underwater observations of James Coe, who again worked from a rubber raft in the backdown area; 3) good environmental conditions; and 4) the skill and dedication of the vessel captain, Manuel Jorge, and his crew members. A full report on this cruise will be published in the next issue (39:6) of *Marine Fisheries Review*. The results of the behavioral research under the direction of Kenneth Norris will be reported elsewhere.

ACKNOWLEDGMENTS

We are indebted to NMFS gear specialists, Richard McNeely and Jerry Jurkovich, and the members of the Porpoise/Tuna Interaction Program at the Southwest Fisheries Center for counsel and advise. We are also most grateful to the captains and crew members who cooperated in 1975 porpoise apron tests. Three fishermen, Harold Medina, Joseph Scafidi, and Julius Zolezzi, in particular have made major contributions to the development and introduction of small-mesh net modifications for porpoise safety. Frank Alverson, Vice President of Living Marine Resources, Inc., and August Felando, Director of the American Tunaboat Association, have provided or confirmed historic facts on the fishery. William Evans took the official U.S. Navy photographs of the *Gina Karen* backdown, and we are indebted to the captain of that vessel, Louis Romani, for his cooperation. Art work has been done by Kenneth Raymond and typing of the manuscript by Lorraine Prescott.

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Calif. Fish and Game 63(4): 204–209. 1977

THE ACUTE TOXICITY OF SIX MONOCYCLIC AROMATIC CRUDE OIL COMPONENTS TO STRIPED BASS (*MORONE SAXATILIS*) AND BAY SHRIMP (*CRAGO FRANCISCORUM*)[1]

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The acute toxicities of benzene, toluene, ethylbenzene, p-xylene, m-xylene, and o-xylene were determined for striped bass and bay shrimp by static bioassay. The 96-hr LC$_{50}$'s ranged from 2.0 to 11 µl/l (ppm) for striped bass and from 0.49 to 20 µl/l (ppm) for bay shrimp. Solubilities of these aromatics were determined by gas chromatography in 16 C (61 F) seawater with a salinity of $25^{\circ}/_{\circ\circ}$ as part of our procedure for dosing the animals. The solubilities were 1400, 330, 180, 180, 210, and 230 µl/l (ppm), respectively, which is high enough to be lethal to striped bass and bay shrimp. The toxic effect of the aromatics was more latent in shrimp than in fish as demonstrated by the difference in the 24- and 96-hr tests.

INTRODUCTION

Fish and aquatic invertebrates in San Francisco Bay are continuously being exposed to crude oil and its refined products as a consequence of the many petroleum spills occurring every year in the bay (U.S. Coast Guard Reports 1971–1975[2]). Due to the petroleum chemicals in the bay and the programs initiated to clean it up, the acute and chronic effects of petroleum products on the marine biota in San Francisco Bay are of interest.

Aromatic hydrocarbons, being among the more toxic fractions in petroleum, are receiving much attention; this is especially true with the polycyclic aromatics some of which are carcinogenic. Aromatics are cyclic compounds containing one or more unsaturated rings, benzene being the simplest in the homologous series. Our research efforts were directed toward the monocyclic aromatics for several reasons: their mammalian toxicities (Stecher 1968; and American Petroleum Institute 1960*a*, 1960*b*, 1960*c*); relatively high composition in crude oils and its products (Goldstein and Waddams 1967); the excess production of aromatics by reforming crude oils (Horne and McAfee 1960); and water solubilities (Mackay and Wolkoff 1973; and Benville and Korn 1974). Six monocyclic aromatics were chosen for static bioassays with striped bass (*Morone saxatilis*) and bay shrimp (*Crago franciscorum*). The six aromatics—benzene, toluene, ethylbenzene, p-xylene, m-xylene and o-xylene—predominate in the aromatic fraction of many crude oils (Goldstein and Waddams 1967; and Anderson et al. 1974). The striped bass was chosen, because it is an important recreational fish in this region; the bay shrimp is a popular bait and an important food organism for striped bass and other fishes in the bay. Bioassay information was needed as a preliminary step to studies of chronic effects of aromatics.

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[1] Accepted for publication September 1976.

[2] Pollution Incident Reporting System (PIRS), computer printouts available through U.S. Coast Guard, 12th District, 630 Sansome St., San Francisco, CA 94111

MATERIALS AND METHODS

Mature bay shrimp (mean weight 1.8 g, 0.063 oz) were acquired from a local bait dealer and juvenile striped bass (mean weight 6.0 g, 0.21 oz) from the Bureau of Reclamation fish diversion facility at Tracy, California. The animals were acclimated in seawater (Korn 1975) for one week before transferring the animals into bioassay tanks (180-liter or 48 gal fiberglass aquaria). The salinity and temperature of the seawater was 25°/$_{oo}$ and 16 C (61 F), respectively, which are representative of bay conditions.

Saturated aromatic solutions were prepared by shaking seawater with an excess of the aromatics in a 20-liter (5.3 gal) polyethylene carboy for three 10-second intervals and allowing the mixture to settle for 1 hour. After gas chromatographic analyses of the saturated solutions, the proper volume was mixed into the bioassay test aquaria, each containing ten animals. A 100 ml (3.38 oz) water sample was taken from the bioassay test aquaria at 0-, 24-, 48-, 72-, and 96-hour intervals for analysis. The water samples were extracted with 9.7 ml (0.33 oz) TF Freon (trichlorotrifluoroethane) in a separatory funnel and a 3–4 μl aliquot of the Freon extract injected into a Micro-Tek 220 gas chromatograph equipped with a dual flame ionization detector. Two 6-foot columns were used at 105 C (221 F)—a 5% Bentone 34 and 10% didecylphthalate on 80/100 chromosorb PAW, and a 5% SP-1200 and a 5% Bentone 34 on 100/120 supelcoport. The first column was used for quantifying benzene, and the second was used for quantifying the other five aromatics. Aromatics were considered undetectable below 0.1 μl/l (ppm) for the concentrated extract or 0.01 μl/l (ppm) for the water sample, since the water sample was concentrated by extracting with 1/10th the amount of Freon. The concentration values were corrected by the percent recovery of the first extractions of a 100 ml (3.38 oz) water sample with 9.7 ml (0.33 oz) of TF Freon.[3] All aromatics used were 99+% pure.

TABLE 1. Acute Toxicity of Six Monocyclic Aromatics to Striped Bass and Bay Shrimp at 16 C and 25°/$_{oo}$ Salinity in Static Bioassays

Components	Solubility * (μl/l)	% Extracted w/TF Freon	*Striped bass*				*Bay shrimp*			
			24-hr		*96-hr*		*24-hr*		*96-hr*	
			LC_{50}	95% C.L	LC_{50}	95% C.L.	LC_{50}	95% C.L.	LC_{50}	95% C.L.
Benzene	1400	90	6.9	**	5.8	—	22	20–24	20	19–22
Toluene	330	93	7.3	—	7.3	—	12	10–13	4.3	3.1–5.8
Ethylbenzene	180	82	4.3	3.9–4.7	4.3	3.9–4.7	2.2	—	0.49	0.21–1.2
m-xylene	210	78	9.2	8.3–10	9.2	8.3–10	4.8	3.6–6.3	3.7	2.9–4.7
o-xylene	230	74	11	9.4–12	11	9.4–12	5.3	4.4–6.5	1.3	1.1–1.6
p-xylene	180	78	2.0	—	2.0	—	2.0	—	2.0	—

* Solubility in 25°/$_{oo}$ seawater at 16 C (61 F)

** No confidence limits were calculated from tests without partial mortalities.

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[3] Reference to a trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.

The guidelines for the static bioassays were those outlined by Doudoroff et al. (1951), except for modifications mentioned in this section. The method used to compute the 24- and 96-hour LC_{50} and the 95% confidence limits was described by Litchfield and Wilcoxon (1949). Confidence limits were not calculated for tests without partial mortalities.

Water concentrations were analyzed with a curve-fitting program to describe the volatilization of aromatics over the elapsed time (Hewlett Packard BASIC program modified by Richard Faris at Tiburon Laboratory).

RESULTS

There were toxicity differences between the six aromatics for both the striped bass and the bay shrimp (Table 1). The range in the aromatic toxicities varied more for bay shrimp (.49–22 μl/l, ppm) than for striped bass (2.0–11 μl/l, ppm) at both time intervals (24- and 96-hr). The tolerance of these animals to the six aromatics within the 24-hr period indicated that benzene and toluene were more toxic to striped bass than to bay shrimp. Ethylbenzene, m-xylene and o-xylene were more toxic to bay shrimp than to striped bass for the 24-hr period. P-xylene exhibited the same toxicity for both animals at the 24- and the 96-hr intervals. The "toxicity order" of toluene reversed at the 96-hr interval, toluene being more toxic to bay shrimp. The toxicity of the other aromatics for the 96-hr period remained the same as for the 24-hr period.

Lethal concentrations of aromatics resulted in rapid mortalities of the striped bass. Almost all of the striped bass mortalities occurred within the first six hours of the bioassays. The latent toxic effects were more prevalent with bay shrimp than with striped bass during the testing period. Benzene was the only aromatic that showed a delay in its toxicity to both animals. P-xylene exhibited no difference in toxicity over the two time intervals to both species. Toluene, ethylbenzene, m-xylene and o-xylene were more toxic to bay shrimp at the 96-hr interval than at the 24-hr interval; however, these aromatics exhibited the same toxicity at both time intervals to striped bass.

There was a large difference in the solubility between the monocyclic aromatics in 25°/$_{oo}$ seawater at 16 C (61 F). Benzene was the most soluble (1400 μl/l, ppm) and ethylbenzene and p-xylene the least (180 μl/l, ppm).

The extraction efficiency determined by multiple extractions of the six aromatics from seawater (25°/$_{oo}$ salinity) was high for a 1:10 Freon to seawater ratio. One extraction resulted in recoveries of 74.1 to 93.1%.

The concentrations of the six aromatics in the aquaria decreased linearly each day, in most instances. In some cases the concentrations followed a logarithmic decrease (Table 2). Average percent losses for the four time intervals (24-, 48-, 72-, and 96-hr) were 38, 61, 85, and 96%, respectively.

DISCUSSION

The monocyclic aromatics appear to be moderately toxic to fish relative to other pollutants tested in the past. For example, bioassays with fingerling rainbow trout in fresh water at 12 C (54 F) resulted in the following $LC_{50's}$: Antimycin 30–70 pptr, DDT 8–11 ppb, and acetone 8 ppth.[4]

Striped bass succumbed rapidly to a lethal aromatic concentration with most of the fish expiring within 6 hours. The rapid mortality rate with aromatics in the

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[4] Benville, P. E. Jr., June 1976. *The Acute Toxicity of Nine Hydrophilic Solvents and Their Effect on the Acute Toxicity of DDT to Rainbow Trout.* Unpublished manuscript, pp. 1–13. NMFS, Tiburon Laboratory, 3150 Paradise Dr., Tiburon, CA 94920.

TABLE 2. Percent Loss of Aromatic Concentration in Test Tanks

Compounds	*Initial conc. in µl/l*	*Percent loss*			
	0 hr	*24 hr*	*48 hr*	*72 hr*	*96 hr*
Benzene	3.5	11	34	>99	>99
	5.5	35	53	80	>99
	10	28	51	64	82
	19	37	54	64	82
	22	27	55	66	78
	31	39	—	—	—
	34	38	—	—	—
Toluene	4.5	38	56	>99	>99
	12	41	51	96	>99
	16	44	—	—	—
	21	29	—	—	—
	29	31	—	—	—
Ethylbenzene	1.0	>99	>99	>99	>99
	4.9	67	>99	>99	>99
	5.9	>99	—	—	—
	12	38	—	—	—
	20	40	—	—	—
m-xylene	1.1	21	47	66	>99
	4.7	40	62	89	>99
	8.5	45	66	84	99
	13	35	—	—	—
o-xylene	1.3	32	82	>99	>99
	4.6	33	85	>99	>99
	9.3	23	49	95	>99
	18	33	—	—	—
p-xylene	1.0	19	38	59	>99
	3.9	18	—	—	—
	7.0	21	—	—	—

first few hours of the bioassay has been observed by other researchers (Pickering and Henderson 1966; and Morrow 1974). In contrast, a greater latent effect was exhibited in bay shrimp than striped bass as evidenced by the difference in LC_{50}'s between the 24-hr and 96-hr tests. This delayed effect may be characteristic of invertebrates or of the stage the invertebrates are in (Karinen and Rice 1974). These authors noted a toxicity difference between the 24-hr and 48-hr LC_{50}'s of crab to crude oil in the postmolt stage but no toxicity difference in the premolt stage

It appears that the location of the two methyl groups on the benzene ring affects the toxicity of the xylene isomers. P-xylene with the two methyl groups located at the opposite ends of the benzene ring makes the p-isomer the most stable and the most resistent to detoxification, whereas the ortho arrangement with the two adjacent methyl groups would be the least stable and would be most easily detoxified. This hypothesis held true for striped bass and for the 24-hr bay shrimp bioassays, except for o-xylene at the 96-hr interval. The 96-hr exception in bay shrimp may be explained by the delayed toxic effect of this aromatic on invertebrates.

Aromatics appear to be more toxic to striped bass than to other fingerling fish. Pickering and Henderson (1966) reported on the following LC_{50} values in soft and in hard water for bluegill, flatheads, goldfish and guppies; 22–37 ppm for benzene; 24–59 ppm for toluene; 32–97 ppm for ethylbenzene; and 21–37 ppm for xylene. Our values for 96-hr test ranged from 2.0 to 11 ppm for striped bass. Possible causes for the differences in toxicity values ($LC_{50's}$) could be attributed to bioassay technique. The bioassay technique must be adapted to the chemical and physical properties of the toxicant being tested. This is especially true with compounds that have a high volatility and a low solubility as in the case of the aromatics. In the past, toxicity values ($LC_{50's}$) for aromatics were calculated from the amount of the aromatic poured into the test aquaria. This procedure assumes all of the aromatic goes into solution which we found has not been the case. Only a small portion of the aromatic will dissolve, resulting in a higher LC_{50} value. This problem was overcome by making a saturated solution of the aromatic, analytically determining the concentration of the aromatics, and diluting the saturated solution to the desired concentration. The concentration of the saturated aromatic solution can be duplicated when the salinity and temperature are constant.

It is interesting to note that an increase in salinity lowers the amount of aromatic that will dissolve. For example, the 25°/₀₀ salinity used in the bioassays reduced the concentration of benzene in a saturated solution from 1993 ppm in distilled water to 1400 ppm, and of toluene from 401 to 330 (Benville and Korn 1974). The solubility of benzene was affected the most by the increase in salinity with a 30% reduction in dissolved benzene; toluene solubility was affected less, with an 18% reduction. It appears that, as aromatics become more struturally complex, their solubility is less affected by salinity. The solubility of ethylbenzene and the xylene isomers would propably be even less affected by salinity than toluene. We do not have the solubility data to support this hypothesis, and the reported solubility data cannot be used because of the inconsistencies which are encountered with compounds below the 10,000 ppm in solubility. Gunther, Westlake, and Jaglan (1968) have suggested many reasons for the inconsistencies in solubility data.

Meyerhoff (1975) has reported slightly higher LC_{50} values for benzene and striped bass (10.9 µl/l or ppm for 96-hr). One reason for a higher value is a different technique. The benzene was introduced at a slow rate until the desired concentration was reached. This would reduce the trauma experienced by the fish when they are placed in high aromatic concentrations.

Later work by Neff et al. (1976) which includes quantitative analyses of bioassay solutions yields 96 hr LC_{50} results higher than results we found using a similar type of shrimp (*Palaemeontes*). Their LC_{50} values compared to our results were 27 to 20 µl/l (ppm) for benzene, 9.5 to 4.3 µl/l (ppm) for toluene and 7.4 to 1.3–3.7 µl/l (ppm) with xylenes. The difference in results may be explained by temperature and species differences between the two studies.

The current experiment was based on a single dose test where the concentrations were decreasing over time. The loss of these aromatics in most instances was a linear function when compared to five other functions (exponential, power function, and three hyperbolic functions). The aromatic concentration could not be accurately predicted at any time interval because of uncontrolled variables such as change in biomass from mortalities during the test and fungal and bacterial degradation. The magnitude of these and other losses (volatilization, sorption, etc.) can be determined only by measuring the amount of toxicant left in the water. Then an accurate toxicant exposure level and the persistence of the toxicant in the water are known. Our analysis showed that more than half of the aromatic usually volatilized within 48 hours, with an average biomass of 0.43 g/l (0.056 standard deviation).

ACKNOWLEDGMENTS

We wish to thank Norman Abramson, Izadore Barrett, Louis Di Salvo, Hal Guard, Maxwell Eldridge, Stanley Rice, and Jeannette Struhsaker Whipple for their reviews of our manuscript. Johanna Alban, Barbara Caluori and Alice Jellett have put in many hours in typing many revisions which we deeply appreciate.

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THE CERATIOID FISHES OF THE GENUS *THAUMATICHTHYS*

OSTEOLOGY, RELATIONSHIPS, DISTRIBUTION AND BIOLOGY

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ABSTRACT

On the basis of a total of 26 specimens of the genus *Thaumatichthys*, ranging from larvae to adults, a general description of the genus is presented, including the osteology, dentition, jaw mechanism and illicium and esca structures of the females and a description of the previously unknown male. The genera *Amacrodon* Regan & Trewavas and *Galatheathauma* Bruun are synonymized with *Thaumatichthys* Smith & Radcliffe and it is concluded that the known specimens of this genus represent three species: *T. pagidostomus* Smith & Radcliffe, *T. binghami* Parr, and *T. axeli* (Bruun).

The relationships of *Thaumatichthys* to other genera of Ceratioidei is discussed mainly on basis of a comparative study of a representative of the genus *Lasiognathus* Regan. Diagnosis of the family and keys to its genera and the species of *Thaumatichthys* are provided.

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I. INTRODUCTION

In a bottom haul with a herring otter trawl at 3570 m depth in the east Pacific, the Galathea Expedition caught a fish which the leader of the expedition, Dr. Anton F. Bruun, in the popular report on the cruise (Bruun 1953, 1956) declared "unquestionably the strangest catch of the Galathea Expedition, and altogether one of the oddest creatures in the teeming variety of the fish world" (cf. Pl. 1). Besides data on the catch, he provided a painting of the nearly 450 mm long fish, gave a short general description of the specimen, and named it *Galatheathauma axeli*, a new genus and species of deep-sea angler fishes

(Ceratioidea). Bruun made preparations for a scientific publication to replace this preliminary note but, due to his untimely death in 1961, it was not finished.

Bruun was aware that the most outstanding character of this fish, the position of the light organ (esca) in the roof of the mouth instead of on top of the head and the extreme development of the upper jaw and its teeth, was not quite unique among ceratioids. He wrote (Bruun 1956) "We found that a small specimen, eight centimetres long, of a similar type, had been taken by an American expedition in 1908, in Indonesia in 1385 metres of water ..." This first representative of this kind of ceratioid was described by Smith and Radcliffe (1912). It was a most curious fish which they rightly named "the trap mouthed wonderfish": *Thaumatichthys pagidostomus*. Having the first dorsal fin ray transformed into a lure and lacking pelvic fins, it could be referred to the pediculate fishes of the suborder Ceratioidei. However, in several features it differed to such an extent from the then known species that they placed it in a separate new family, the Thaumatichthyidae. Among other things it was distinguished by the greatly expanded and depressed head, with enormously developed movable premaxillaries which carried long hooked teeth and were anteriorly widely separated, only connected by membranous skin. Furthermore, the bulb of illicium projected from the underside of this membrane just inside the mouth.

The next specimen referred to *Thaumatichthys* was described by Parr (1927). It was caught in a midwater trawl fished with 8000 feet of wire in the western North Atlantic. The specimen differed from the type of *T. pagidostomus* in size (39 versus 59 mm s.l. (standard length)), in development of eyes and teeth, and, according to the description, in number of dorsal fin rays. It was made the type of a new species *T. binghami* Parr, 1927. Regan and Trewavas (1932) placed this species in a separate new genus, *Amacrodon*, solely based on the absence of the pair of very long hooked premaxillary teeth found in the type of *T. pagidostomus*. Parr (1934) accepted this separation when, without description, he reported a second specimen of *"Amacrodon binghami"* caught in the same area as the type specimen.

Bertelsen (1951) tentatively referred to *Thaumatichthys pagidostomus* four larval specimens (4.4 to 24 mm in total length) from the Dana Expeditions, on basis of osteological characters and number of dorsal fin rays.

Finally, Brewer (1973) reported, from off the Pacific coast of Mexico, a catch of a specimen, 22 mm s.l., which he referred to *T. pagidostomus*.

Including the *Galathea* specimen, the total number of hitherto recorded specimens of this group is thus nine, assigned to three species and genera.

When, after Anton Bruun's death, the senior author of this paper (E.B.) took over the study of the *Galathea* specimen, and had the opportunity to compare it with the recorded specimens of *Thaumatichthys* and *Amacrodon*, it became evident that the differences on which the separation in genera were based could be ascribed to differences in age and that they, consequently, all should be referred to *Thaumatichthys* Smith & Radcliffe, 1912. Study of a new specimen obtained by the other author (P.S.) confirmed this, but added to the difficulties in separating the species. More material was needed to be able to judge ontogenetic and individual variation, and partly for this reason publication was postponed. Meanwhile, increased effort in deep-sea research in recent years has resulted in the collection of a considerable number of specimens of this genus, which have kindly been made available for this study.

Including the previously known 9 specimens, the study material consists of 26 specimens, representing stages from larvae of 3 mm s.l. to adults of about 365 mm s.l. Most of the specimens are females. Besides three larval males described by Bertelsen (1951), only a single adolescent male has been obtained. After the study was completed information on 6 additional females was received. Of this total of 32 specimens, 25 were caught in the Caribbean and adjacent Atlantic waters, and only 5, including the type of *T. pagidostomus*, the *Galathea* specimen, and 2 larvae, are from the Indo-Pacific. From this material we have concluded that three species comprise the genus *Thaumatichthys*: *T. pagidostomus*, *T. binghami*, and *T. axeli*.

Acknowledgments

We are most grateful to the following persons and institutions for loans and gifts of specimens:

Richard C. Robins and John C. Staiger, University of Miami, Marine Laboratory (UMML); Harvey R. Bullis, National Marine Fisheries Service, Pascagola (specimens now in USNM); Richard H. Rosenblatt and Carl L. Hubbs, Scripps Institution of Oceanography (SIO); Robert J. Lavenberg, Natural History Museum of Los Angeles County (LACM); Cara Cashman, Department of Oceanography, Texas University; and G.E. Maul, Museu Municipal do Funchal, Madeira. Many thanks are due to colleagues at the U.S. National Museum, Bingham Oceanographical Collection and University of Miami, Marine Laboratory for hospitality and assistance during visits to these institutions. For helpful discussions we are indebted to Theodore W. Pietsch, Museum of Comparative Zoology, Harward University, and Jørgen Nielsen, Zoological Museum, University of Copenhagen.

II. GENERAL DESCRIPTION OF THE GENUS *THAUMATICHTHYS*

A. FEMALES

The most characteristic external features of metamorphosed female *Thaumatichthys* are 1) the broad and depressed head and anterior part of body; 2) the development of the premaxillaries which carry long hooked teeth and are extended far beyond the short lower jaw; furthermore, they are anteriorly widely separated from each other, and are hinged to the skull in such a way that they can be turned up and down; 3) the position of illicium which emerges anteriorly in the roof of the mouth from the ventral side of the membrane which connects the premaxillaries; 4) the presence of a denticle on esca; 5) the position of the tiny eyes close to the corner of the mouth. In shape of head and position of illicium and eyes, *Thaumatichthys* differs from all other ceratioids, and only *Lasiognathus* has similarly developed premaxillaries and denticles on the esca.

The posterior part of the body is somewhat more slender than in most other female ceratioids, and the dorsal fin is relatively well developed. The skin is black or dark brown and carries on the lower part of the head and body numerous small spines.

In the following account those features which may be relevant to the understanding of the relationships, ontogeny, and biology of the members of this genus will be described in more detail.

1. Osteology

The following description is based (A) on an alizarin stained juvenile female of *T. binghami* ZMUC P921948 69.9 mm s.l. Comparative observations (B) were made on the adult holotype of *T. axeli*, 365 mm s.l. which is nearly completely skinned. On some of the other specimens, including the types of *T. pagidostomus* and *T. binghami*, observations were made on X-ray photographs and on superficial bones, either through the skin or through incisions in this. Finally, comparisons were made with the alizarin stained larval male described by Bertelsen (1951). Except for ontogenetic differences, the skeletons of the examined specimens were extremely alike in nearly all details.

Cranium (Fig. 1). A. The skull is short and very flat. In percent of its length, from anterior margin of vomer to posterior margin of epiotics, the greatest depth is hardly 20, greatest width at sphenotics and pterotics 75, width of vomer 58 and smallest interorbital width 28. The ethmoid cartilage is a triangular solid plate, covering the anterior part of the parasphenoid and the broad vomer, and dorsally bordered and partly covered by the slender anterior parts of the frontals and the lateral ethmoids. Anteriorly it forms in each side semispherical swellings which protrude between the lateral wings of vomer and the expanded heads of the lateral ethmoids, and articulate laterally with the palatines and maxillaries, and anteriorly with the prolonged articular process of the premaxillaries (cf. Figs 2 and 17). No symphysial cartilage of the upper jaw could be observed, and no supraethmoid ossification (= the mesethmoid of Regan & Trewavas 1932, Bertelsen 1951, and others - cf. Pietsch 1972) is developed.

Each of the lateral ethmoids consists of a broad cup-shaped head which is rigidly attached to the ethmoid cartilage, and a relatively slender conical shaft which at its posterior thicker end is anchylosed ventrolaterally on the anterior part of the frontals.

The vomer is broad, about 75% of the greatest width of the skull. Its anterior margin is medially concave, and its ventral surface is smooth and toothless.

The frontals are widely separated and anteriorly narrowly pointed without a notch at the base of the lateral ethmoids. The parietals are small, triangular or nearly drop-shaped, with the posterior end drawn out into a slender point and overlapping the

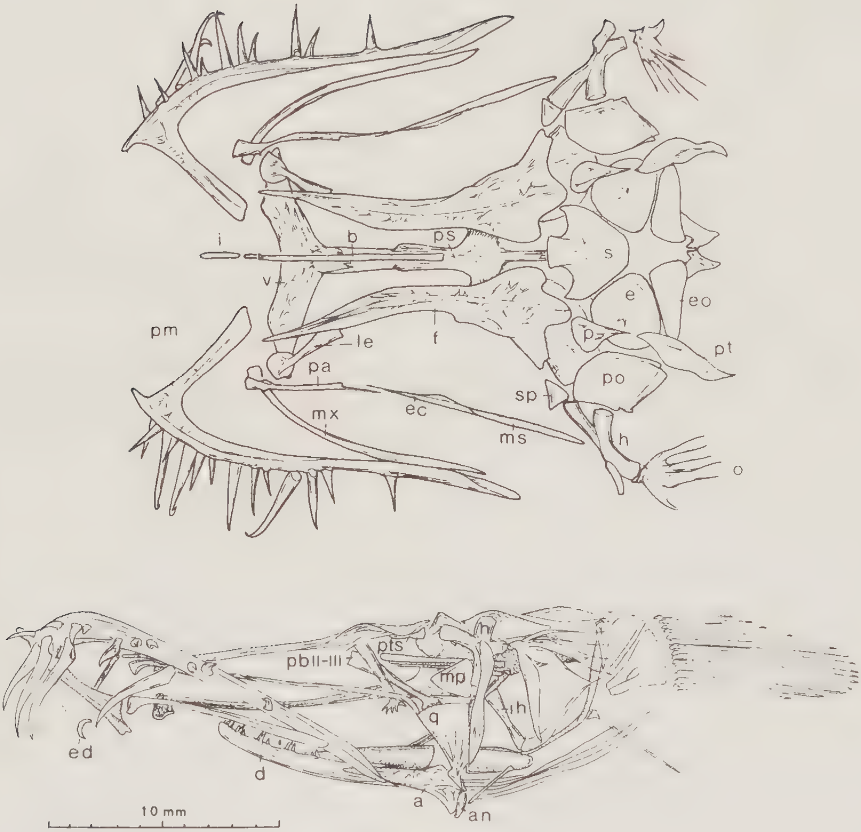


Fig. 1. Skeleton of head of *Thaumatichthys binghami* 69.9 mm (ZMUC P 921948) in dorsal and lateral view. (a: articular, an: angular, b: pterygiophore of illicium, d: dentary, e: epiotic, ec: ectopterygoid, ed: denticle of esca, eo: exoccipital, f: frontal, h: hyomandibular, i: illicium, ih: interhyal, le: lateralethmoid, mp: metapterygoid, ms: mesopterygoid, mx: maxillary, o: operculum, p: parietal, pa: palatine, pb II-III: pharyngobranchials, ps: parasphenoid, pm: premaxillary, po: pterotic, pro: prootic, pt: posttemporal, pts: pterosphenoid, q: quadrate, s: supraoccipital, sp: sphenotic, v: vomer).

epiotics. Small pterosphenoids are present. The conical sphenotics are very small, while the pterotics, epiotics, supraoccipital and exoccipitals are well developed. The epiotics do not meet behind the supraoccipital.

As no dissection of the specimen was made, the bones forming the floor and lower sides of the skull, prootics, exoccipitals, basioccipital, and posterior part of parasphenoid were not studied in detail.

B. As far as could be observed without staining of the 22.6 mm female larva (LACM 31107, Fig. 15), its head skeleton was quite similar to that of the 18.5 mm larval male, showing that at this stage no sexual dimorphism in the osteology had developed except for the presence of a small upward directed illicium on the snout of the female and the presence of two tiny denticlelike ossifications at the tip of the basal bone and the base of the illicium of the male (Bertelsen 1951). The frontal bones of the larvae are much broader than those of the metamorphosed specimens. They meet medially, carry wide lateral laminae above the well developed eyes, and are anteriorly notched at the base of the lateral ethmoids. Furthermore, the vomer of the larval male carries four well developed teeth. (Their possible presence in the unstained female larvae could not be ascertained). Like in the stained 69.9 mm specimen, no supraethmoid is developed; the sphenotics are very small, the parietals are posteriorly pointed, and each of the posttemporals has a posterior long saillike extension. The skull of the large adult specimens differs in the normal way from the larvae and juveniles in the stronger ossification of the bones which overlap or are strongly connected in irregular sutures; the epiotics meet behind the supraoccipital. In the 365 mm holotype of *T. axeli* a small supraethmoid could be observed as an almost circular bony plate medially on the large ethmoid cartilage (Fig. 2).

Mandibular arch. A. The premaxillaries are very long and strongly ossified bones which are situated in a very forward position on the head. They are slightly S-curved and carry series of more or less long, hooked teeth (cf. p. 15).

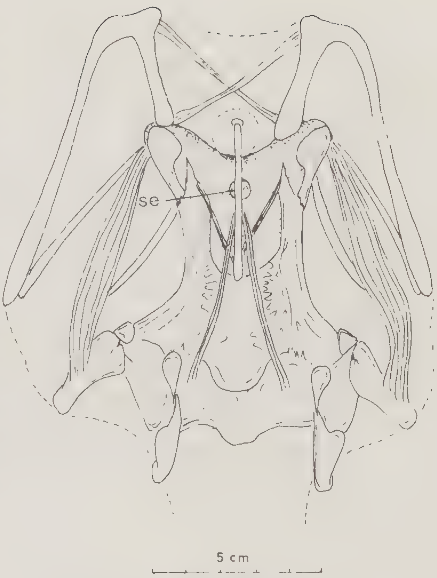


Fig. 2. Skeleton of head of *Thaumatichthys axeli*, holotype, 365 mm. (Ethmoid cartilage dotted; se: supraethmoid).

Each has at the anterior end a short, slightly upturned spine representing the ascending process, and behind this an extremely long, mediocaudally directed, articular process. The heads of the premaxillaries and their processes are widely separated. They lack a symphysial cartilage and are connected only by membranous tissue, and more indirectly by a pair of elastic bands connecting each ascending process with the anterior end of the maxillary and palatine of the opposite side (Figs 2 and 17). For further details on the premaxillaries, cf. the section on jaw mechanism (p. 29).

The maxillaries are thin, slender bones, each with a small, nearly undivided head attached by ligaments to the head of the palatine and the proximal end of the elastic band mentioned above.

In ventral view the lower jaw forms a nearly exact half-circle. In lateral view its length is only about half of the total length between the angular spine and the tip of the premaxillary. The dentaries are relatively weakly developed and lack a symphysial spine. As in the premaxillaries, the teeth are arranged in regular series (cf. p. 18). A labial cartilage (cf. Pietsch 1972) is present posteriorly,

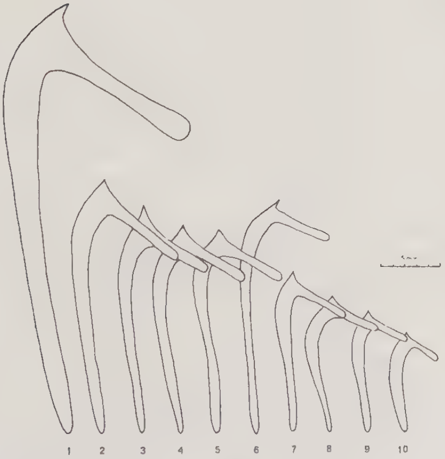


Fig. 3. Left premaxillary of *Thaumatichthys binghami* (1,2, 4,5, and 7-10), *T. axeli* (3), and *T. pagidostomus* (6), arranged according to standard length of specimens: 1) 145.5 mm, 2) 87.1 mm, 3) 85.2 mm, 4) 73.1 mm, 5) 69.9 mm, 6) 60.0 mm, 7) 57.2 mm, 8) 51.5 mm, 9) 45.0 mm, 10) 40.0 mm.

connecting the dentary with the premaxillary and maxillary. The articular carries a very small spine behind the articulation with the quadrate.

B. In the larvae the premaxillaries do not extend beyond the lower jaw, their heads meet, and each has an ascending process which is as long or longer than the articular process. The length and shape of premaxillaries were examined in a number of specimens representing all three species (Fig. 3 and App. Table 1, p. 38). In the larval stages its length is 11-15% s.l., in the 36.5 mm juvenile holotype of *T. binghami* it has increased to 18% s.l., and in all the larger (40 to 293 mm s.l.) specimens of this species it ranges from 23.4 to 26.3% s.l.

The premaxillary lengths of the two specimens of *T. axeli* fall within the upper end of this range (25.6% and 26.5% s.l.). In the holotype of *T. pagidostomus* it is distinctly longer, being 32.8% s.l. As shown in Fig. 3, it furthermore differs in shape from the others, being anteriorly more curved and having a sharper, more medial directed anterior spine. The change in number and length of teeth with increase in the size of specimens will be described in a separate section below.

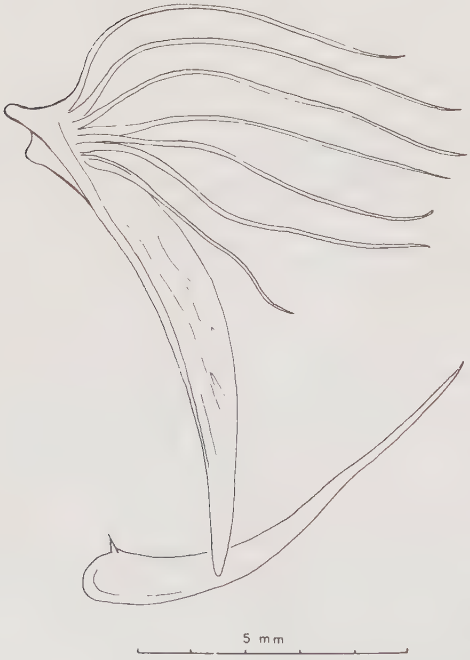


Fig. 4. Opercular bones of *Thaumatichthys binghami*, 142.5 mm (ZMUC P 921950).

Palatine arch. A. The triangular metapterygoids are well developed, while the palatines, meso- and ectopterygoids are very thin and elongated.

Hyoid arch. A. In connection with the small depth of the head and the great width between angles of the lower jaw, the hyomandibular-symplectic-quadrate arch is directed outwards, forming an acute angle with the horizontal plane.

The hyomandibular has a double head and a well developed posterior process articulating with the operculum. The symplectic is thin and slender. The interhyal and quadrate are well developed, the latter with a small oblique, ventrocaudally directed spine. Epihyals, ceratohyals, dorsal and ventral hypohyals are well developed. The ceratohyal is long and carries six branchiostegal rays, the first two well spaced medially on the bone, while the last four are closely set on its posterior, broader end.

Opercular bones (Figs 4 and 5A). A. The preoperculum is a narrow, oblong bone, closely connected with the lower arm of the hyomandibular, the symplectic, and the posterior upper part of the quadrate.

In the stained specimen the operculum is divided into six radiating branches. The lowermost branch is separated from the five upper branches by a wide notch, and has a broad, posterior, membranous flange. Similar, but smaller flanges are present at the base of the upper branches which distally taper into slender rays. The suboperculum is long, posteriorly tapering into a very slender backwardly curved tip. The anterior end is truncated and carries dorsally a tiny, anteriorly directed spine. The interoperculum is long and narrow, with a small posterior flange at its upper end.

B. The shape of operculum and suboperculum could be observed in a number of specimens. It was found that the branching of the operculum exhibited variation. The larval male (Bertelsen 1951) has a total number of nine radiating branches, of which the two behind the strong lowermost branch are ventrally directed and partly enclosed in its membranous posterior flange. The upper six branches are closely set and separated from the lower ones by a broad notch. In the 22.6 mm female larva

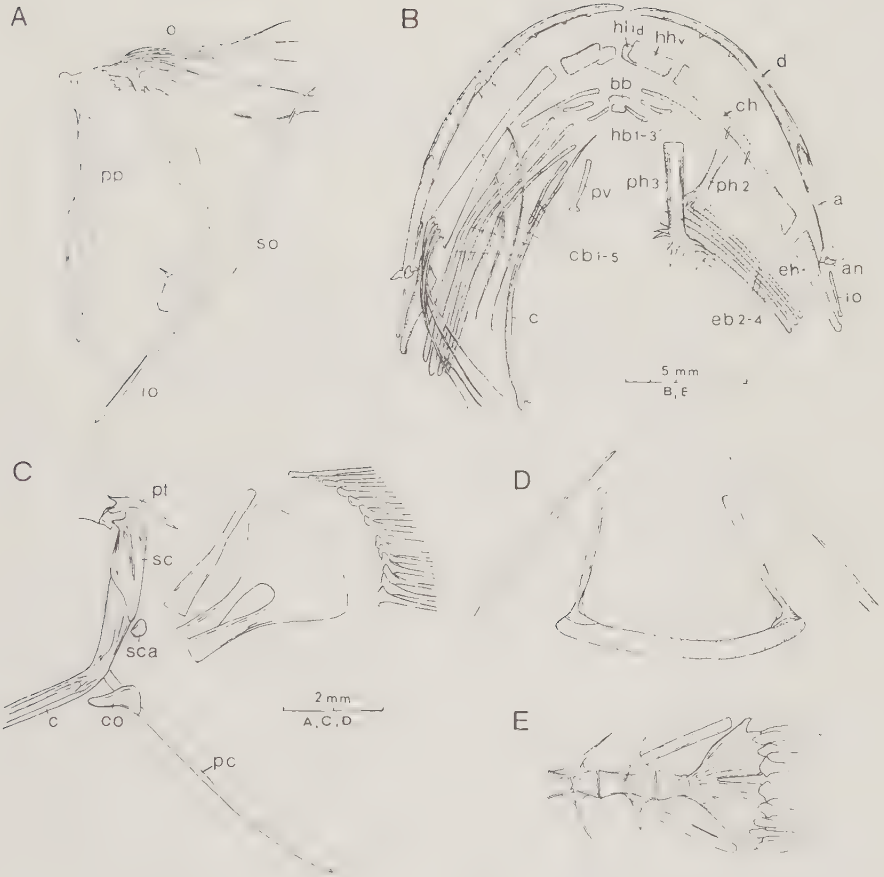


Fig. 5. Skeleton of *Thaumatichthys binghami*, 69.9 mm (ZMUC P 921948). A, opercular bones (io: interopercle, o: opercle, pp: preopercle, so: subopercle); B, branchial arches and adjacent bones (a: articular, an: angular, bb: basibranchial, c: cleithrum, cb 1-5: ceratobranchials, ch: ceratohyal, d: dentary, eb: epibranchials, eh: epihyal, hb 1-3: hypobranchials, hh-d and hh-v: dorsal and ventral hypohyal, ph 2-3: pharyngobranchials, pv: pelvic bone); C, skeleton of pectoral girdle and fin (c: cleithrum, co: coracoid, pc: postcleithrum, pt: posttemporal, sc: supracleithrum, sca: scapula); D, pelvic bones; E, caudal skeleton.

there is a total of 13 radiating ribs, of which the six uppermost ones are well developed free rays while the following six are less distinct and more or less enclosed in the posterior flange of the strong lowermost branch. In the 36.5 mm type of *T. binghami* there are six free upper rays, while no distinct ribs or rays are present in the broad flange of the lower branch. In the 40 mm *T. binghami* only four distinct upper rays could be observed. The 142 5 mm *T. binghami* (Fig. 4) has seven upper rays, of which the base of the lowermost is fused with the flange of the strong lower branch. The branching of the operculum in *T. pagidostomus* and *T. axeli* seems to fall within this variation, but in each of the three specimens the fragile branches have been broken, and less developed rays or ribs have been lost.

There are five or six upper rays present in the type of *T. pagidostomus*, six in the type of *T. axeli*, and five in the 85.2 mm specimen of this species.

The suboperculum tends to become more slender and relatively longer with increasing size of the specimens. The small anterodorsal spine is present in all the examined specimens including the holotype of *T. pagidostomus* and both specimens of *T. axeli*.

Branchial arches (Fig. 5B). A. The very large third pharyngobranchial carries 10 recurved teeth and the somewhat smaller second pharyngobranchial 6 teeth.

B. Like the teeth in the jaws, the number and length of teeth on the pharyngobranchials increase with increasing size of the specimens from respectively 4 and 5 in the 2nd and 3rd pharyngobranchials in the 45.0 mm specimens to 15-17 and 24-25 in the holotype of *T. axeli* (cf. App. Table 1).

No first epibranchial and first pharyngobranchial could be observed. The remaining epibranchials II to IV, and the anterior four ceratobranchials are long and thin. The 5th ceratobranchial is only about one-third of the length of the others. None of them carries tooth plates. Three hypobranchials and a single basibranchial ossification are present.

Pectoral girdle (Fig. 5C). A. The posttemporals are narrow, blade-shaped bones pointed at both ends; the anterior ends overlap the epiotics, while the posterior ends protrude freely as sail-like extensions of the roof of the skull. The supracleithrum and the upper descending part of cleithrum are relatively short and robust, while the lower anteriorly directed part of cleithrum is very long and thin. The ventroposteriorly directed postcleithrum is slender and slightly curved upwards.

The coracoid is small and no ossification of the scapula could be observed. There are three pectoral radials. The uppermost first radial is a simple, slightly conical rod without expansion of its thin distal end, while the two lower radials are widely expanded distally and fused.

B. The larval male has three well separated pectoral radials, the lowermost two of about the same size and somewhat larger than the uppermost. As described above, the expanded distal ends of the two lowermost radials are fused in the 69.9 mm specimen (Fig. 5C). In the 142.5 mm *T. binghami* this fusion is nearly complete, only a short narrow split remains of their separation (Fig. 6A), and in the 293.5 mm *T. binghami* and the 365 mm holotype of *T. axeli* the fusion is complete (Fig. 6B).

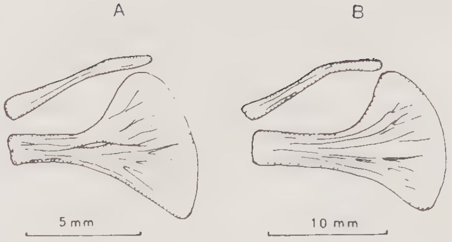


Fig. 6. Pectoral radials. A, *Thaumatichthys binghami*, 142.5 mm (ZMUC P 921950); B, the holotype of *T. axeli*, 365 mm.

Pelvic bones (Fig. 5D). A. The pelvic bones are small, slender rods with slightly expanded distal ends. They are widely separated and their posterior ends are connected with a long, slightly curved band of cartilage.

Illicial apparatus (Fig. 1). A. The pterygiophore (the basal bone of illicium) is relatively short (14.3% s.l.) and completely hidden by the skin of the head. The illicium bone is very short (3.2% s.l.) and downward directed behind the crossing elastic bands in the menbranous tissue connecting the premaxilliaries. The esca carries a curved denticle, pointed at both ends. The rudiment of the second cephalic ray is situated close to the anterior end of the basal bone. (For further details cf. p. 19).

Fin rays. A. In the stained specimen there are seven dorsal rays carried by the same number of pterygiophores, four anal rays carried by three pterygiophores, nine (2 + 4 + 3) caudal rays carried by a single hypural plate, deeply notched between the bases of the upper four and lower five caudal rays (Fig. 5E). The neural and haemal spine of the last free vertebra (the second preural centrum) are greatly enlarged. Each of the pectoral fins has 15 rays.

B. There is little variation in number of fin rays in the examined specimens, and no significant differences between the three species of *Thaumatichthys* were found. All specimens examined have four anal rays and nine caudal rays. The following variation in ray counts was noted. The single specimen of *T. pagidostomus* has 7 dorsal rays and 15 and 16 pectoral rays. The two specimens of *T. axeli* have 6-7 dorsal rays and 14-16 pectoral rays. The 17 specimens of *T. binghami* have 6-7 dorsal rays and 14-16 pectoral rays. The five larvae not assigned to species have 6-7 dorsal rays and 14-15 pectoral rays. Parr (1927) reported the holotype of *T. binghami* to have four dorsal fin rays; however, the anterior two rays are almost completely hidden by the skin and the correct count is six.

2. Dentition of jaws

As the previous separation into species and even genera of the known species of *Thaumatichthys* was based on differences in their development of the premaxillary teeth, a detailed examination is required of the individual, ontogenetic and specific variation in this character. For this purpose the premaxillary (in most cases the left) of each specimen was drawn, the length of each tooth was measured and its position in the pattern of series was determined. The results are summarized in Fig. 8 and Tables 1 and 2.

The two female larvae, 6.3 and 22.6 mm, have relatively short, conical, slightly curved teeth arranged in a double series, about 8-12 in each premaxillary and about 8-10 in each dentary. No trace of these larval teeth could be observed in the smallest metamorphosed specimens of 36.5 and 40.0 mm s.l. (BOC 2015 and 3713), in which all the teeth in the jaws are in early stages of development and have soft, unossified bases (Fig. 7A).

The premaxillary teeth of all of the metamorphosed specimens are arranged in a very distinctive pattern consisting of six overlapping, oblique longitudinal series (Figs 7 and 8). The first tooth of each of the six series are spaced along the edge of the jaw in the young specimens. The second tooth of each series develops slightly in front, ventromedial to the first tooth of the following series, the third in front and inside the second tooth of the following series, etc., forming in this way oblique transverse series sectioning the longitudinal series. In each series, the longitudinal as well as the transverse, the teeth increase in length in both the caudad and mediad directions. The teeth are slender, conical, and more or less recurved. The larger teeth of series II to IV are especially strongly hooked.

The last developing teeth of each series are placed inside the edge of the jaw, and until they have reached their full length and are ossified at the bases they tend to be depressed towards the roof of the mouth. As will appear from the diagramme (Fig. 8) such teeth frequently terminate the oblique, longitudinal series and are found only in this position in the tooth patterns. When fully developed, they are raised and become depressibly hinged to the edge of the premaxillary bone, and with increasing age and growth of the bone they are gradually displaced upwards on the side of this. In later stages they become fixed, and finally the oldest and smallest teeth of each series lose function, become covered by skin, and may be more or less imbedded in the jaw bone or disappear completely.

In the two largest specimens of *T. binghami*, 225 and 293.5 mm s.l. where at least some of the series appear to be complete, the number and position of missing teeth can be extrapolated. In the 365 mm holotype of *T. axeli*, a greater number is missing. By comparison of the length of teeth with those in the corresponding series of the smaller specimen of *T. axeli* and the series of *T. binghami*, the best agreement is obtained if it is assumed that the anteriormost tooth of the best represented series in the *T. axeli* holotype (series III to V in the right jaw) represents tooth number 2 (cf. Fig. 8u-v).

As will appear from the figures and the summary in Table 1, there is an increase in number of teeth with increasing length of fish within the observed size range of specimens, i.e., from 10 to 15 in each premaxillary of the specimens less than 60 mm; 14 to 22 in specimens between 60 and 100 mm, 24 to 31 in the two specimens between 100 and 150 mm, 37 to 46 in the two specimens of 225 to 293 mm, and 54 to 55 in the 365 mm specimen if the 10 to 11 assumed lost teeth are included. Variation occurs; in some specimens the teeth are further developed than in others of similar length. For example, the 225 mm UMML 30958 with 45 teeth is in this respect ahead of the 293.5 mm USNM 214571 with 37 and 38 teeth in each side of the jaw.

In the number of premaxillary teeth and their distribution in each series, neither the holotype of *T. pagidostomus* nor the smaller specimens of *T. axeli* differ significantly from *T. binghami* of equal size. Similarly, the largest of the known *Thaumatichthys* specimens, the holotype of *T. axeli*, is in this respect in good accordance with the observed developmental series.

In the first fully developed teeth (I 1, and the first 3 to 5 of series II-VI) the variation in length of corresponding teeth is relatively small in the best represented species (*T. binghami*). The largest and latest

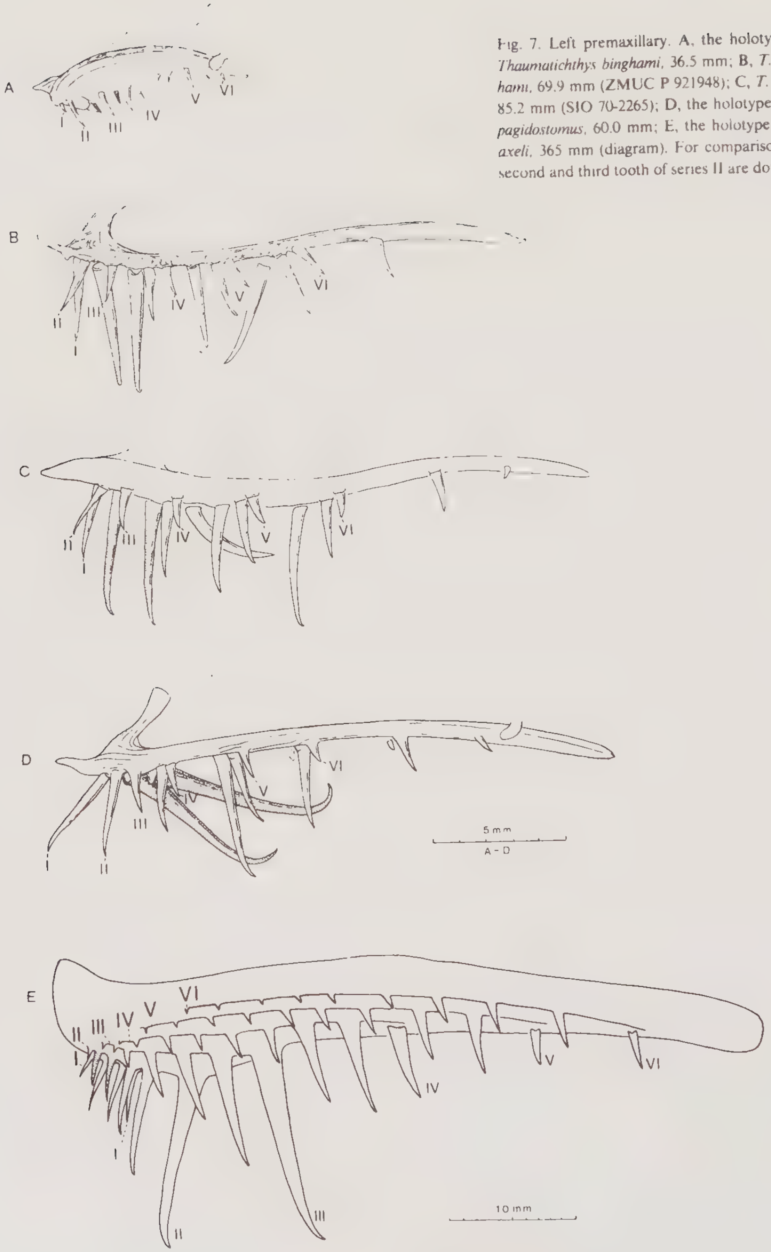
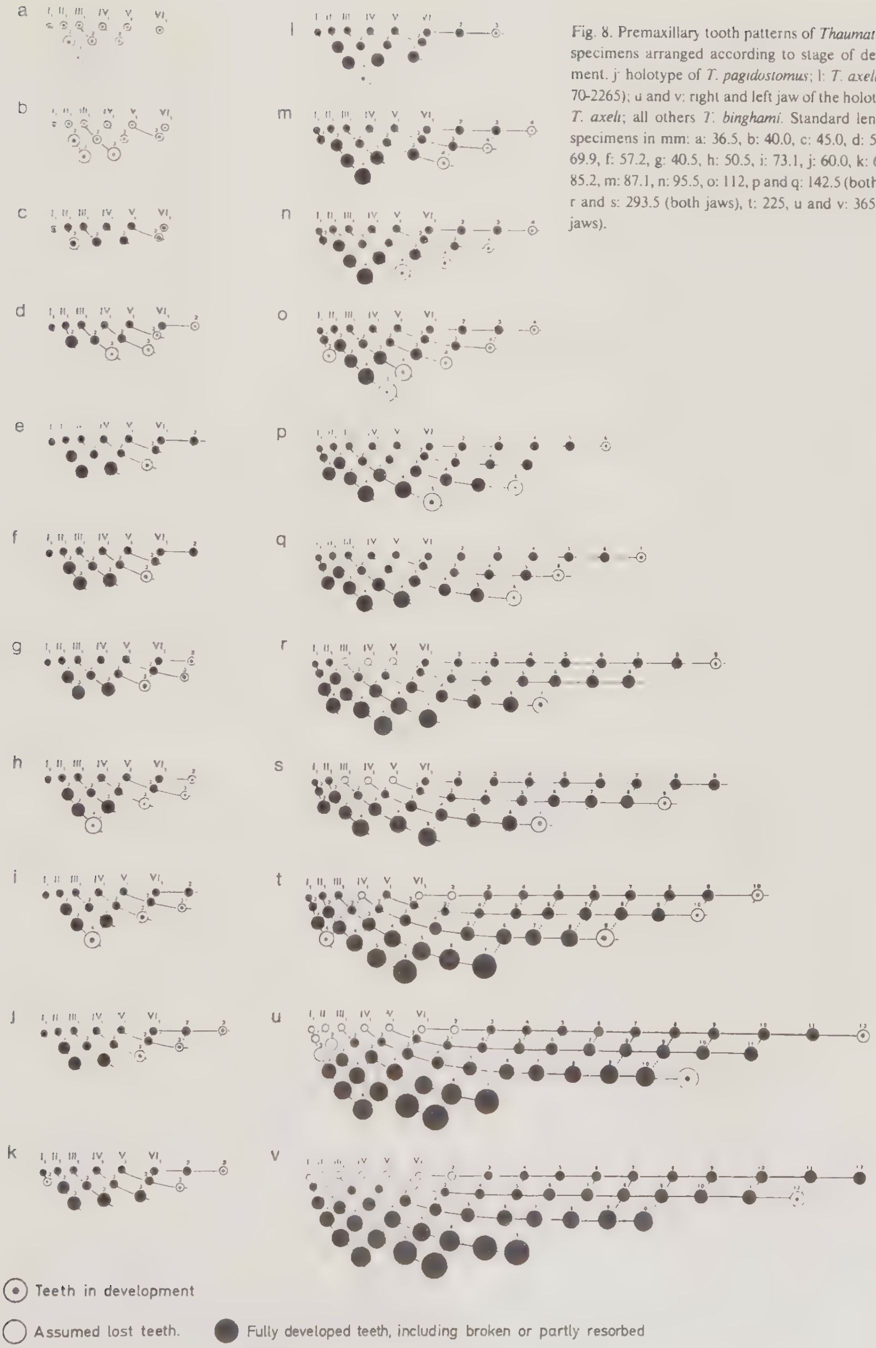


Fig. 7. Left premaxillary. **A**, the holotype of *Thaumatichthys binghami*, 36.5 mm; **B**, *T. binghami*, 69.9 mm (ZMUC P 921948); **C**, *T. axeli*, 85.2 mm (SIO 70-2265); **D**, the holotype of *T. pagidostomus*, 60.0 mm; **E**, the holotype of *T. axeli*, 365 mm (diagram). For comparison the second and third tooth of series II are dotted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u
v
I, II, III, IV, V, VI
Teeth in development
Assumed lost teeth.
Fully developed teeth, including broken or partly resorbed

Fig. 8. Premaxillary tooth patterns of *Thaumatichthys* specimens arranged according to stage of development. j: holotype of *T. pagidostomus*; l: *T. axeli*, (SIO 70-2265); u and v: right and left jaw of the holotype of *T. axeli*; all others *T. binghami*. Standard length of specimens in mm: a: 36.5, b: 40.0, c: 45.0, d: 51.5, e: 69.9, f: 57.2, g: 40.5, h: 50.5, i: 73.1, j: 60.0, k: 67.0, l: 85.2, m: 87.1, n: 95.5, o: 112, p and q: 142.5 (both jaws), r and s: 293.5 (both jaws), t: 225, u and v: 365 (both jaws).

Table 1. No. of premaxillary teeth in oblique longitudinal series I-VI. Incompletely developed, broken and assumed lost teeth included.

species:	*binghami*	*pagidost.*	*binghami*	*axeli*	*binghami*	*binghami*	*binghami*	*axeli*
mm s.l.:	36.5-57.2	60.0	67.0-73.1	85.2	87.1-95.5	112-142.5	225-293.5	365
no. specimens:	7	1	3	1	2	2	2	1
								l r
series I	1	1	1 - 2	1	2	3	3 - 4	6 - 6
II	2 - 4	3	3 - 4	4	4	4 - 5	4 - 6	7 - 7
III	2 - 3	3	3	3	3 - 4	4 - 5	5 - 7	8 - 7
IV	2 - 3	3	3	3	4	4 - 6	7 - 9	10 -11
V	2 - 3	3	2 - 3	2	4	4 - 6	8 -10	12 -11
VI	1 - 2	3	2 - 3	3	4	4 - 7	9 -10	12 -12
total:	10 -15	16	14 -16	16	21 -22	24 -31	37 -46	55 -54

developed teeth of the largest specimens show greater variation. All specimens show the very regular increase in tooth length in each series, but comparison of corresponding teeth of the different specimens shows considerable variation. Table 2 gives a summary of the lengths of these first developed teeth of each series which are most numerously represented in the material. In spite of the variation found in the *T. binghami* specimens, the holotype of *T. pagidostomus* differs very significantly from *T. binghami* in this character. Of the 13 teeth which are fully developed in this specimen, 8 are distinctly longer than the longest corresponding teeth found in *T. binghami*, and the remaining 5 are near or above the average length of the corresponding teeth of this species.

The length of each tooth of the 85.2 mm *T. axeli* (SIO 70-2265) is within the observed range of the corresponding tooth in *T. binghami*, and in most cases remarkably close to the average length of these. No conclusion can be drawn from a comparison of the tooth lengths of the holotype of *T. axeli* with those of *T. binghami*. As mentioned above, most of the first developed teeth are missing in the large specimen, and the remaining of these are more or less reduced in length by wear, resorption, and imbedding in the jaw bone. The length of the corresponding later developed large teeth present only in this specimen and the three largest *T. binghami* varies greatly without any indication of difference between the two species.

The teeth of the lower jaw (Fig. 9) are shorter and less curved than those of the upper jaw. Like the premaxillary teeth they increase in number and length with increasing size of the specimen, varying from 9-10 and a greatest length of 1.2-1.5 mm in the smallest, to 22-30 and 5.6-10.3 mm in the three largest *T. binghami*, and 39-40 and 10.5 mm in the holotype of *T. axeli*. They are arranged in distinct anteromedial series, each of two to four teeth of increasing length with the smallest outermost as in the premaxillaries. No specific differences in the pattern, number or length of these teeth could be observed.

Table 2. Length of anterior premaxillary teeth in oblique longitudinal series I-VI. Incompletely developed or broken teeth not included.

			binghami		*axeli* (SIO 70-2265)	*pagidostomus* (holotype)
Tooth	no.	no. speci mens	range	av.		
I	1	14	2.2-3.5	2.75	3.0	3.8
II	1	17	1.1-2.3	1.88	1.9	3.0
	2	16	3.0-5.6	4.25	4.5	6.5
	3	16	3.8-5.8	4.81	4.8	7.0
III	1	14	1.1-1.8	1.36	1.1	1.5
	2	16	0.8-2.3	1.81	1.9	3.3
	3	13	1.8-3.4	2.75	2.5	4.3
IV	1	15	0.6-1.5	1.06	1.0	1.4
	2	17	0.9-2.3	1.68	2.0	2.4
V	1	14	0.6-1.4	1.02	0.9	1.0
	2	14	0.8-2.6	1.78	2.4	3.4
VI	1	14	0.8-1.6	1.14	0.8	1.3
	2	13	0.8-1.9	1.52	1.6	1.5

Fig. 9. Lower jaw of *Thaumatichthys binghami*, 69,9 mm (ZMUC P 921948).

3. Illicium and esca

In the female larva 6.3 mm s.l. the tiny club-shaped illicium protrudes on top of the head above the anterior margin of the eye which at this stage is large and in normal position (Bertelsen 1951). In the 22.6 mm specimen (Fig. 15) the illicium has moved forward and protrudes on the snout in front of the eye and a short distance above the symphysis of the upper jaw.

At metamorphosis the anterior ends of the premaxillaries become separated and are prolonged beyond the tip of the lower jaw. Anteriorly they are connected by a membranous fold of the skin of the snout. The articulation between illicium and its pterygiophore is imbedded in this fold and surrounded by a small bulb of connective tissue. The illicium projects from the underside of this membrane, a short distance behind its incurved anterior edge, which is supported by the crossing pair of elastic bands connecting the ascending process of each premaxillary with the anterior end of the maxillary and palatine of the opposite side (cf. Fig. 17). These ligaments are most probably derivatives of the subcutaneous connective tissue and appear to develop during metamorphosis.

In the specimens of less than about 50 mm, the esca is carried on a short free illicial stem as described and figured by Parr (1927). In the larger specimens it becomes sessile with the skin of its base confluent with that of the membrane.

The pterygiophore (or basal bone) of the illicium is short (about 15% s.l.) and lies in the shallow groove between the anterior ends of the frontals. Its retractor and exertor muscles are very thin and weakly developed.

In descriptions of the structure of ceratioid escas the terms "anterior" and "posterior" assumes an erect position of illicium. The upside-down esca of *Thaumatichthys* is best observed in an anteroventral view (Figs 10 and 12) in which the anterodorsal oriented part, which in the following will be termed "upper", corresponds to "posterior" in other esca descriptions.

In all the *Thaumatichthys* specimens, the esca consists of the following elements:

1) An internal black bulb-shaped photophore with an unpigmented distal field of varying size.
2) A low, more or less pigmented base, confluent with the pigmented skin of the short illicium stem or, in older specimens, directly with the membranous skin fold.
3) A distal lobed, somewhat inflated, unpigmented disc, more or less distinctly divided into an upper pair of lateral wings and a lower median broad tongue. The lower lateral angles of this tongue are drawm out into a pair of pointed, tentacle-like lobes, and one or two similar pairs are formed by extensions of the lateral wings.
4) A curved denticle imbedded in the lower median tongue. (This structure is missing in some specimens).
5) Two simple, median appendages close to each other on the upper part of esca. The uppermost of these is short, tapered, and unpigmented in all the examined specimens. The second, more distally positioned appendage. is untapered, more or less pigmented, and of extremely variable size in the different specimens.

The ontogenetic and individual variation of the esca in the specimens here assigned to *T. binghami* is illustrated in Fig. 10A-P, in which all the escae are shown in anteroventral view and drawn to the same scale except for the two largest for which a half as large magnification was used.

There is no distinct change in the relative size of the esca with increasing length of fish. The diameter of the internal bulb varies between 2.1% and 4.0% s.l. in the specimens. The unpigmented field of this bulb varies in size from a relatively narrow split (e.g. Fig. 10D, K and N) to a wide oval, covering the main part of the distal surface (Fig. 10J). This indicates that the light from the photophore can be varied by changing the contraction of this field. No opening of the luminous gland of the inner bulb could be observed on the outer surface of esca. If present, the pore is extremely small and undistinguishable in the semitransparent, more or less folded skin on the upper part of esca at the bases of the unpaired appendages where it should be expected.

The pointed lateral lobes vary in number. However, most of the specimens with standard length

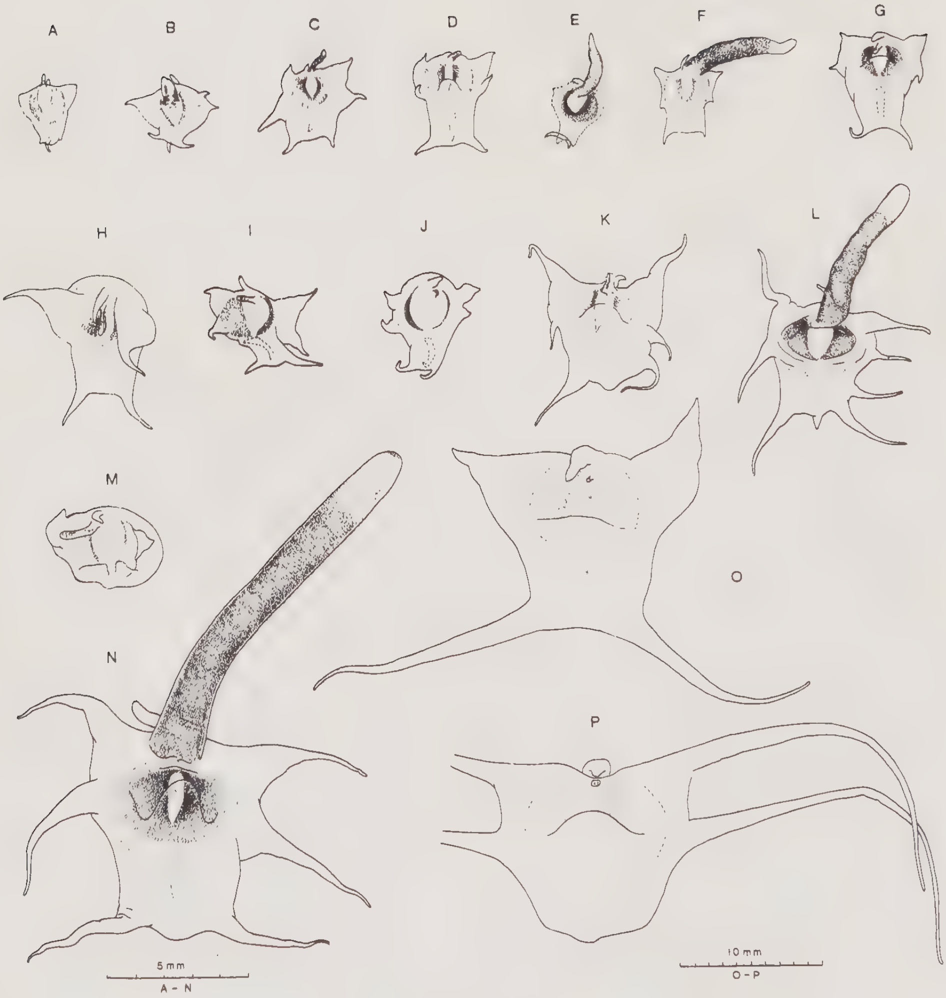

Fig. 10. Escae of *Thaumatichthys binghami* in anteroventral views. A, 40.0 mm (BOC 3713); B, 40.5 mm (UMML 30866); C, 45.0 mm (Texas Univ. 69A-11-91); D, 50.5 mm (UMML 31363); E, 51.5 mm (USNM 214570); F, 58.0 mm (UMML 31362); G, 57.2 mm (UMML 26927); H, 67.0 mm (UMML 30926); I, 69.9 mm (ZMUC P 921948); J, 73.1 mm (ZMUC P 921947); K, 95.5 mm (UMML 30930); L, 87.1 mm (USNM 214571); M, 112 mm (UMML 27394); N, 142.5 mm (ZMUC P 921950); O, 225 mm (UMML 30958); P, 293.5 mm (USNM 214571).

between 50 and 142.5 mm (Fig. 10C-N) show a basic pattern of three pairs; two upper pairs on the lateral wings and one pair on the median tongue. The exceptions are: 1) the 51.5 mm USNM specimen (Fig. 10E), in which the outer skin of the esca is torn, 2) the 112 mm UMML specimen (Fig. 10M), in which the lobes are represented by low irregular folds and may be in a state of regeneration, 3) the 87.1 mm USNM specimen (Fig. 10L) which, in addition to the three pairs, has an additional, lateral, pointed lobe on the left side at the base of the median tongue and, furthermore, a median short pointed lobe at the tip of this between the lowermost pair, and 4) the 67.0 mm UMML specimen (Fig. 10H) which, like the youngest specimens described below, has a single pointed lobe on each lateral wing.

The esca of the juvenile 40 mm BOC specimen (Fig. 10A) is extremely similar to that of the 39 mm holotype of *T. binghami* described and figured by Parr (1927). In these specimens only the upper angles of the lateral wings are slightly pointed, and the median tongue carries a pair of very small points. In the 45 mm specimen from Texas University (Fig. 10B), all three lobes are developed on the left side, while the right lateral wing has a single point only.

In the two largest specimens, the 225 mm UMML specimen (Fig. 10O) and the 293.5 mm USNM specimen (Fig. 10P), the esca differs from the smaller specimens in having only two pairs of lateral lobes. Furthermore they differ from each other in the position and development of these. In the UMML specimen, the lobes seem to represent the uppermost and lowermost pair of the smaller specimens. Each of the broad lateral wings ends in a single short point, while the pair on the median tongue is prolonged into slender tentacles.

In the USNM specimen, both pairs of lobes are prolonged into slender tentacles and, according to their position, they seem to represent the lobes of the lateral wings of the smaller specimens, while the median tongue is short and without lobes.

The median appendage which is uppermost in the illustrations is short and unpigmented in all the specimens, and varies from a tiny wart (Fig. 10D) to a length of about half the diameter of the internal bulb (Fig. 10H).

The pigmented second median appendage shows extreme variation in development. In 8 of the 11 specimens less than 75 mm s.l. and in the 112 mm specimen with the esca in an apparent state of regeneration, this appendage is of similar thickness and as long as or only a few times longer than the uppermost appendage and carries relatively few scattered melanophores. In five specimens, [the 40.5 mm UMML 30866 (Fig. 10B), the 51.5 mm USNM specimen (Fig. 10E), the 58 mm UMML 31362 (Fig. 10F) and the 87.1 mm and 142.5 mm ZMUC specimens (Fig. 10L and N)], this appendage is much thicker than the upper appendage and increases greatly in relative length with increasing lengths of the specimens. In the smaller of these specimens, it has a length of about half the diameter of the inner bulb, in the intermediate from 1½-2½, and nearly three times the bulb diameter in the largest specimen. These enlarged appendages are heavily pigmented except for the distal transparent tip. In the 95.5 mm UMML 30930 (Fig. 10K), this appendage is torn.

Finally, the two largest specimens of 225 and 293.5 mm (Fig. 10O and P) both differ from all the others in having only a tiny wartlike rudiment of this appendage, each with a few remaining melanophores.

In 11 of the 17 examined specimens, including the smallest as well as the largest one, a well developed 1-2 mm long, curved denticle could be observed in the median tongue of esca (Fig. 11). The denticle is pointed at both ends. The distal end protrudes as a small hook on the dorsocaudad oriented back of the median tongue.

In six specimens no spine could be found by external examination of this semi-transparent organ. However, a very thin bony remnant of the denticle was found by superficial dissection of the esca of the 225 mm specimen. In two of the others, the spine may be lost (the specimen with esca in apparent regeneration (Fig. 10M) and the 87.1 mm USNM specimen (Fig. 10L), in which the skin of the back of

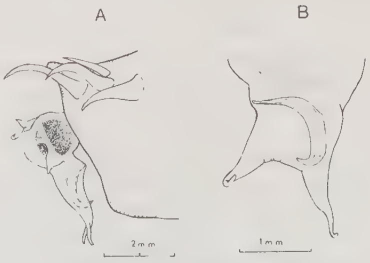

Fig. 11. Escae of *Thaumatichthys binghami*. A, lateral view of a 57.2 mm specimen (UMML 26927); B, median tongue of esca of a 69.9 mm specimen (ZMUC P 921948).

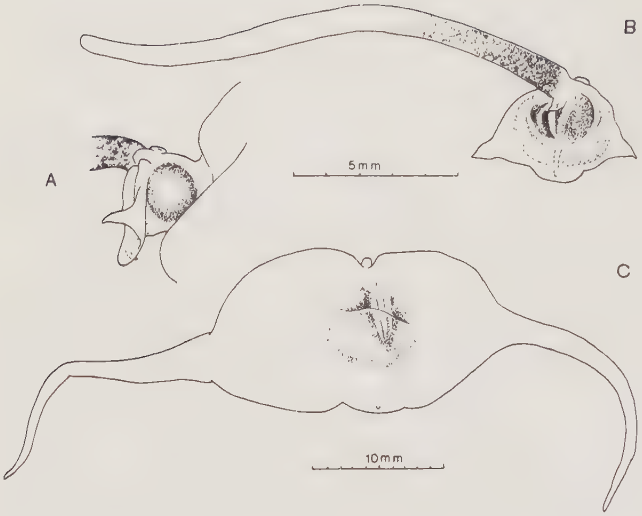

Fig. 12. Escae of *Thaumatichthys axeli*. A and B, 85.2 mm (SIO 70-2265), in lateral and anteroventral views; C, the 365 mm holotype.

the esca tongue is slightly torn), but in the well preserved escae of the remaining three specimens (Fig. 10F, H, and K), the lack of denticle can hardly be explained as artifacts.

In both specimens of *T. axeli*, the escae differ from those of *T. binghami* in three characters: 1) only a single pair of lateral pointed lobes is present, 2) the uppermost median appendage is represented by an untapered, small wart, and 3) the median tongue is represented by a low crest without pointed lobes (Fig. 12). This tongue encloses an approximately 2 mm long, curved denticle in both specimens.

In the 85.2 mm SIO specimen (Fig. 12A and B), the lower angle of each lateral wing is drawn out into a short, pointed lobe. In the 365 mm holotype (Fig. 12C) this pair of lobes is prolonged into slender tentacles.

In the SIO specimen the second median appendage is stout, untapered, and 15 mm long or about five times as long as the diameter of the bulb. The proximal third of the appendage is pigmented. In the holotype only a low indistinct unpigmented wart represents this appendage.

In the holotype of *T. pagidostomus*, the esca is damaged; only the inner bulb with the loosely attached 2.1 mm long, curved denticle remains. Smith & Radcliffe describe (1912, p. 580) the illicium and esca as "a slender pedicel bearing at its tip a sharp toothlike process that curves backward". In their illustration, the esca is pictured as a simple small globe with the denticle protruding at the tip. However, the fact that no lobes or appendages on esca are mentioned or pictured need not indicate that the species differs from other *Thaumatichthys* in this character. In their figure, the esca has a diameter of about 1% s.l. or somewhat less than the present diameter of the inner bulb, which is now 1.0 mm or 1.7% s.l. This might indicate that the damage to the esca occurred during capture.

4. Sense organs

As normal in female ceratioids, the relative size of the eyes of *Thaumatichthys* is largest in the young larvae and their growth is nearly stopped after metamorphosis. In the 6.3 mm larva (Bertelsen 1951), the diameter of the pigmented eyeball (the choroid) is 0.9 mm or 14% s.l. In the 18.5 mm specimen the diameter has increased to 1.5 mm (8% s.l.) which is about the same size as in the recently metamorphosed 36.5 mm holotype of *T. binghami*. In all the metamorphosed specimens of 40 to 142.5 mm, the diameter of the pigmented eyeball varies between 1.2 and 1.9 mm, with a slight increasing trend with increasing length of fish; in the three largest specimens (225-365 mm s.l.), this diameter is 2.3-2.5 mm. This stagnation of growth corresponds to a decrease in the relative size of the eye from a diameter of 3.0% to 4.4% s.l. in the four specimens of less than 50 mm to 0.7%-0.8% s.l. in the two largest specimens (cf. Appendix Table 1). The structure of the eye of the holotype of *T. axeli* is described by Munk (1964) and the external examination of the present material shows full agreement with this description. In spite of the extremely small relative size of the eyes in the larger specimens, no indication of degeneration could be observed. In external view they seem very similar to those of female ceratiids as described by Munk (1964, 1966), with a thick transparent sclera and a relatively very large lens located behind the iris. In the best preserved specimens a narrow, anterior, aphakic aperture can be observed.

In the larvae the eyes are in the normal lateral position, filling the space between the short snout, the frontals and the normally developed upper maxillary muscles, levator maxillae superioris (Fig. 15). With metamorphosis the snout and upper jaws are greatly prolonged, and similarly the levator maxillae superioris increase greatly in size and length; the eyes are displaced backwards and downwards into a position below the levator maxillae superioris and closely above the angles of the mouth, where they protrude slightly on the sides of the broad and flat head (Pl. 2). As a result of this displacement of the eyes, the optic nerves and the very feeble eye muscles cross the lateral surface of the strong levator maxillae (cf. Fig. 17A).

In the larval females the relatively well developed olfactory organ is placed in the narrow space between the eye and the heads of maxillary and premaxillary (Fig. 15). With metamorphosis it follows the displacement of the eye, remaining in a position closely anteroventrad to this. In the metamorphosed specimens, the olfactory organ is raised on a somewhat rectangular lobe with the nostrils at the distal corners (Plate 2 and Fig. 7A and D). The lobe is about twice as long as broad, and has a relative length of about 2% s.l. or about half the eye diameter in the smallest specimen, and two to three times this diameter in the largest. In most of the specimens this nasal papilla is preserved in a downward directed position, hanging over the posterior end of the premaxillary near the angle of the mouth.

Four series of lateral line organs can be distinguished: 1) the lateral line of the body posteriorly extends to the base of the caudal fin, and continues on the head in 2) the supraorbital, 3) the suborbital, and 4) the mandibular series. No preopercular series could be observed. Each organ consists of a small elongated untapering papilla arising from the center of a small, white spot in the skin. The papillae are unpigmented at tip and more or less pigmented at base. The organs are connected in series by thin, more or less distinct white lines (Pl. 2). In most of the series the papillae are very small, with a slight tendency to increase in size anteriad on snout and lower jaw. However, in the suborbital series the anteriormost 10-15 papillae are greatly enlarged, forming a very distinctive series of flabs extending along the posterior third of the upper jaw, below the nasal papilla and slightly beyond the eye. The largest of these papillae are about one-fifth of the length of the nasal papilla.

Numerous white-tipped papillae of similar appearance, and presumably belonging to the same sensory system, are present in the roof of the mouth, especially in its anterior part in front of the lower jaw on both sides of esca. The largest of these papillae are arranged in three groups along the ventral side of each premaxillary (Pl. 2). The largest and anteriormost of these groups is situated below the base of the articular process of the premaxillary and close behind the anteriormost teeth. It consists of 10-15 white-tipped stout papillae closely set on a low, somewhat ridge-shaped common base. Their greatest height, including the base, is about the same as the length of the nasal papilla or about 2% s.l. The second of these groups consists of 4-5 papillae which, in the older specimens, are raised on a common stout stem. The posteriormost group consists of a more variable number of papillae, and may be absent in the younger specimens. In the older ones it contains 5-8 irregularly arranged papillae, some of which are separate and others are raised on one or two stems, each with two or more papillae. Single, much smaller papillae, are scattered over the roof of the mouth between the enlarged groups and are most numerous posterior to these.

5. Ovaries

All the examined specimens are immature. In the two largest specimens the ovaries consist of a pair of relatively thin-walled sacks, each about 50 mm long and 15 mm in greatest width in the 365 mm holotype of *T. axeli*, and about 30 x 6 mm in the 293.5 mm *T. binghami*. In both specimens the slightly folded walls of the ovaries are covered with a single layer of oocysts 0.05-0.1 mm in diameter.

6. Skin and color

Spines are present in the skin of the lower part of the body in all the metamorphosed specimens. In the youngest, they are restricted to the opercular region of the head and the ventral side of the body, except for the caudal peduncle where they reach the dorsal midline. With increasing size of specimens the spines gradually cover the ventral side of the lower jaw, a greater part of the body sides, and the anal and caudal fin rays. The skin of the dorsal side of the head, the pectoral and dorsal fins and a posteriad tapering field of the back, remains naked. Each spine arises from the center of a more or less circular plate. The spines are conical, acute, straight or slightly curved, and usually of a length of about half the diameter of their basal plate.

The spines increase in number and size with increasing size of the specimens, but decrease in relative size. The diameter of the c. 10 largest spine plates in a field of about the same relative size on the same locality on the side of the body, was measured in series of specimens (Fig. 13). In the smallest specimen, a 40 mm *T. binghami*, this diameter varied between 0.35 and 0.5 mm or 0.9%-1.3% s.l., while in the 293.5 mm specimen of this species as well as in the 365 mm holotype of *T. axeli*, it was 0.9-1.4 mm or 0.25%-0.45% s.l.

The relative diameters of these spine plates were found to be distinctly larger in the 60 mm holotype of *T. pagidostomus* than in *T. binghami* specimens of the same length, while those of the two specimens of *T. axeli* fall within the variation observed in *T. binghami*.

In the most recently preserved specimens, the color of the skin is dark brown to velvet black. The part of the roof of the mouth which extends beyond the lower jaw is brown, while the walls of the mouth cavity enclosed by this jaw are nearly or completely unpigmented.

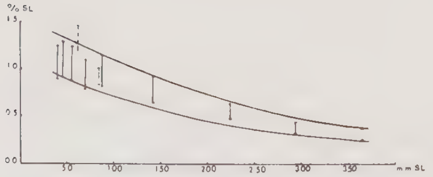

Fig. 13. Diameter of spine plates in percent of standard lengths (cf. text). (—— *T. binghami*, - - - - *T. pagidostomus*, and . . . . *T. axeli*).

B. MALES

The only previously known males of *Thaumatichthys* are 3 larvae of 4.4, 6 and 24 mm in total length, described by Bertelsen (1951). The largest of these is probably at a stage approaching metamorphosis, according to its relatively advanced testes and the fact that it was caught in a pelagic net fishing at a depth of about 1500 m.

Like most of the female specimens made available to us, the single adolescent male ZMUC P 921946 (Fig. 14A) was obtained in the Tongue-of-the-Ocean Programme of the University of Miami. It was caught on 10 May 1973 at station CI 89, 24°47'N, 77°39'W in a semi-balloon trawl fishing at the bottom at a depth of 1938 m. It is 45 mm in total length, 31 mm in standard length.

In general appearance and body proportion (Table 3) it is similar to most other metamorphosed ceratioid males, differing from females in its lack of esca, slender shape, pointed snout with hooked denticles at the tip of the jaws, and enlarged olfactory organs.

In order to preserve this unique specimen for future studies (comparisons with the still unknown *Lasiognathus* male, etc.) it was not cleared, and was stained with an alizarin-alcohol solution only at the snout. Combined with superficial dissection the more important osteological features could in this way be observed (Fig. 14C-E and G). The tip of the jaws carries 4 upper and 7 lower denticles (Fig. 14E-G). Those of the upper jaw are arranged in two bilateral symmetrical pairs. The denticles of the upper pair are the largest, 1.3 mm long, and ventrolaterally curved. Those of the lower pair are more strongly hooked, with the distal end curved downwards and the sharp tips thus pointing backwards nearly parallel to their slender shafts. In each side the two denticles are closely set, and their somewhat expanded bases are indistinctly separated, while no connection between the bases of those of left and right side is present. They are carried mainly by the head of the premaxillary at the place of its undeveloped ascending process. Otherwise the premaxillary is of normal appearance, with well developed, mediocaudal directed, articular processes and without any trace of resorption, except for the complete lack of teeth.

The maxillaries are similarly well developed. The head of each carries two processes, the inner and shorter of which is turned underneath the articular process of the premaxillary, and the other lies

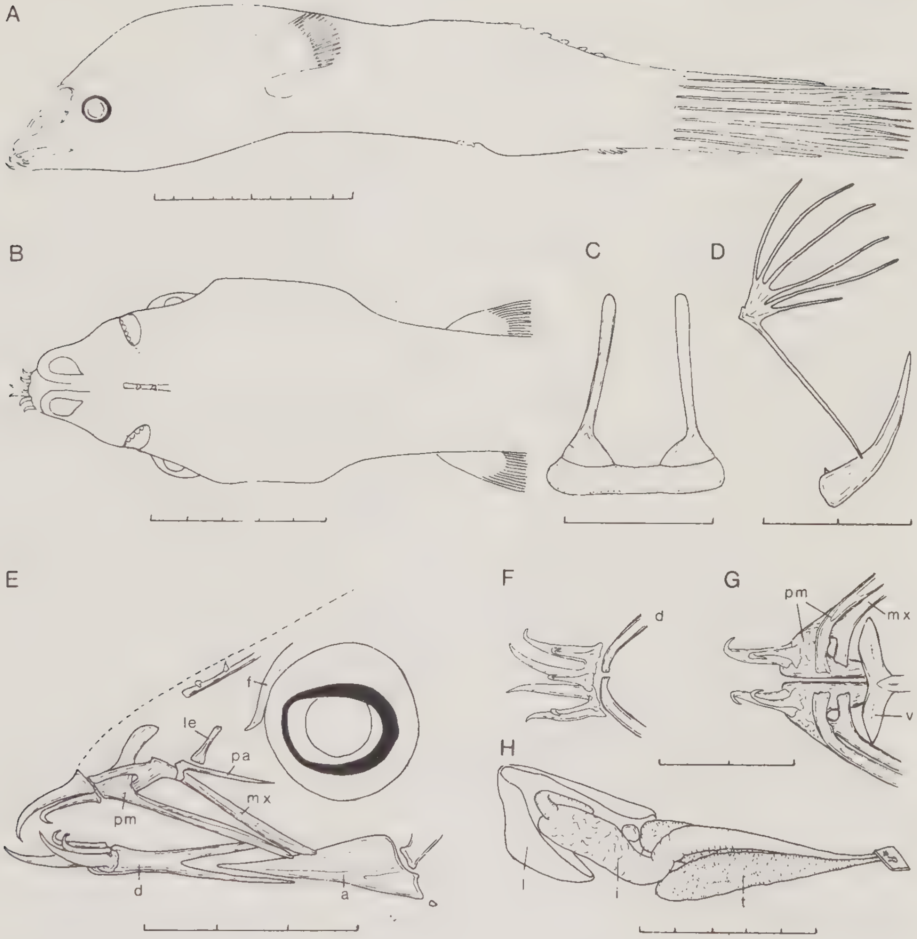

Fig. 14. Male of *Thaumatichthys* (?) *binghami*, 31 mm. A, lateral view; B, dorsal view of head (torn skin and broken fin rays reconstructed); C, pelvic bones; D, operculum and suboperculum; E, skeleton of jaws; F, denticles of lower jaw in dorsal view; G, denticles on tip of upper jaw in ventral view (abbreviations in E-G as in Fig. 1); H, viscera (i: intestine, l: liver, t: testes).

close to the outer surface of this process, reaching the base of the uppermost denticle.

The seven denticles of the lower jaw are arranged in two bilateral, symmetrical series: a lower and outer row of four large denticles with dorsolaterally curved, pointed tips - and an inner series of three shorter denticles placed just above the spaces between the 4 larger ones. Like the lower pair of the upper jaw, the three shorter denticles have slender shafts and similarly hooked tips. The somewhat expanded bases of these seven lower denticles are fused and by connective tissue attached to the tips of the dentaries. As in the premaxillaries, no teeth or traces of teeth sockets are present.

The frontals are broad and short, and their lateral, anterior tips are behind the posterior ends of

Table 3. Measurements of males.

	adolescent mm	larva mm
Total length	45	24
Standard length	31	18.5
% of s.l.	%	%
Tip of snout to gill opening	42	42
Length of snout	12.0	5.4
Width between sphenotics	19.4	21.6
Length of upper jaw*	9.7	12.0
Length of lower jaw*	16.1	16.8
Diameter of pigmented eyeball	5.2	8.6
Horizontal diameter of olfactory organ	ca. 10	ca. 5
Greatest depth of head	26	ca. 54
Greatest depth of body	22.5	ca. 54
Longest ray of caudal fin	45	40
Longest ray of pectoral fin	10	18.5

* Denticles not included

the lateral ethmoids (Fig. 14E). The pterygiophore of illicium is short and has no connection with the denticle and jaw mechanism. It carries rudiments of illicium and the second cephalic ray, but no trace could be found of the denticlelike, minute bone formations observed by Bertelsen (1951) on each side of the illicium in the larval male.

The operculum and suboperculum (Fig. 14D) have the shape characteristic to the genus. The upper part of operculum is divided into 6 radiating slender branches, and suboperculum is posteriorly tapering into a slender curved tip, and anteriorly truncate with an anterodorsal spine.

The posterior ends of the pelvic bones are expanded and connected by a band of cartilage (Fig. 14C), which is folded in such a way that the pelvic bones are very closely set (artificially stretched out in the illustration).

The numbers of fin rays are: D 6, A 4, C 9 and P 15-15.

Both eyes have circumlental aphakic apertures. In the right eye the pupil and retinal cup are nearly circular, but oval in the left one (Fig. 14E), probably due to shrinking (for this reason corrected in Fig. 14A). The diameter of the pigmented part of the right eye is 1.6 mm (5.2% s.l.). The diameter of the transparent outer coat of the eyeball is 2.1 mm.

The olfactory organs are very large, about 3 mm (c. 10% s.l.) in horizontal diameter, each with 13 olfactory lamellae. The covering skin, including the bridge between the nostrils, is torn, but, as reconstructed in Fig. 14A and B, the posterior nostril is much larger than the anterior.

The skin contains numerous small spines scattered over the body from the occipital region to the base of the caudal fin. In the preserved specimen it is dark brown. Subdermally the head and body are covered with a layer of dusky pigment of nearly uniform density.

The vicera is shown in Fig. 14H. The liver is relatively small. Oesophagus is narrow, and the nearly straight intestine empty. The testes are immature, each about 6.5 mm in total length and 1.2 mm in greatest width.

A comparison with the 18.5 mm s.l. male larva shows the main features of the male metamorphosis. As shown in Table 3, the most significant changes in relative body proportions are a prolongation of the snout and a reduction of the depth of head and body. The relative length of the pectoral fin is somewhat reduced, while the length and width of head and length of jaws and caudal fin are about the same. The larva has small teeth in the jaws, three in each premaxillary and five in each side of the lower jaw, and no denticles.

The eyes of the three larvae are circular and lack aphakic aperture. During the larval development they increase in actual size but decrease in relation to the standard length, from more than 15 to less than 9%. According to the comparison with the adolescent male, the growth of the pigmented eyeball stops at metamorphosis. Its actual diameter is the same (1.6 mm) in the 18.5 mm larva as in the 31 mm adolescent male.

The olfactory organs of the 18.5 mm male are slightly larger than in the smaller larvae, but in height only about 5 per cent of the standard length, and the nostrils are tiny.

The club-shaped testes of the 18.5 mm specimen are in beginning development but only about 0.5 mm in greatest diameter, and in estimated volume about 10% of those of the adolescent male. Compared with this, its liver, stomach and diameter of oesophagus are considerably larger. In linear dimensions the liver is about twice and in estimated volume about 8 times that of the 31 mm specimen.

Considering the much more slender shape of the adolescent male, these reductions might indicate that the feeding of the male is nearly or completely arrested after the metamorphosis of the jaw mechanism.

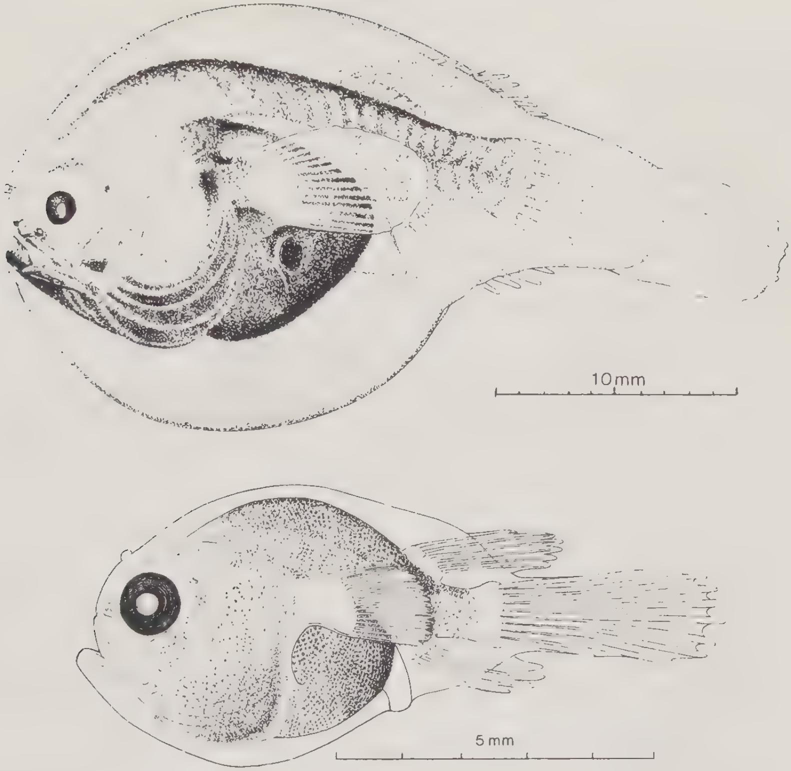

Fig. 15. Female larvae of *Thaumatichthys*. Above, 22.6 mm (LACM 31107-1). Below, 6.5 mm (*Dana* St. 3999, from Bertelsen 1951).

C. LARVAE

Bertelsen (1951) tentatively referred four larvae, 4.4, 6, 10 and 24 mm in total length, to *Thaumatichthys pagidostomus*. Comparison of his description of the osteology of the largest of the specimens with that of the adolescents and adults here presented, confirms the correctness of the reference to this genus. This appears from several characters, and, in particular, from the presence of a multiradiate operculum which, among ceratioids, is found only in *Thaumatichthys*.

Furthermore, these larvae differ from all other known ceratioid larvae in that the subdermal pigment layer covers the whole surface of head and body with concentrations along the margin of the gillcover, on peritoneum, and on the back. There is less or no pigment on the pectoral lobes and at the base of the caudal fin. Scattered small melanophores are present in the outer transparent skin.

The female larva, LACM 31107-1 (Fig. 15), recorded by Brewer (1973), fits this description. It is somewhat larger, 34.1 mm in total length (22.6 mm s.l.), than the largest of the previously known specimens, and, in accordance with this, the pigmentation of the outer skin is more densely pigmented. Its meristic and morphometric characters are given in App. Table 1.

Bertelsen's (1951) specific identification of the larvae was based on the assumption that *T. binghami* had only four dorsal fin rays as by mistake stated by Parr (1927). As no significant differences in pigmentation or other characters between the larvae from different areas could be found it has not been possible to refer them to species.

III. DISTRIBUTION

The known 32 records of *Thaumatichthys* indicate a worldwide distribution of the genus in the tropical zones of the oceans (Fig. 16). The holotype of *T. pagidostomus* was caught in the Gulf of Tomini, off Sulawesi (Celebes). The holotype of *T. axeli*, the second specimen referred to this species, and one larva came from the eastern Pacific between lat. 09° and 32°N close to the American west coast. The type of *T. binghami*, the 22 other metamorphosed females referred to this species, the metamorphosed male, and one of the larvae are all caught between lat. 10° and 30°N in the Gulf of Mexico, the Caribbean Sea, and the adjacent Atlantic waters off the Bahamas. Finally, two larvae were collected in the eastern central Atlantic off the Gulf of Guinea, and one larva in the Indian Ocean in the southern part of the Mozambique Channel. Except for the two larvae which were caught 450-500 miles off the African coast, all the specimens came from positions less than 250 nautical miles from land.

Of the 32 specimens representing *Thaumatichthys*, 5 larvae and 3 of the youngest metamorphosed specimens were caught in open pelagic nets fishing well above the bottom, while all the remaining 24 specimens were caught in bottom trawls.

The three smallest larvae (less than 6.5 mm s.l.) were caught in open nets fishing in maximum depths of about 20 to 100 m below the surface. The two larger larvae (18.5 and 22.6 mm) were obtained in nets which had their main fishing depths at about 1500 and 780 m, respectively. Finally, the three young metamorphosed *T. binghami* of 36.5, 40.0, and 45.0 mm were caught in pelagic hauls with estimated maximum depths of 1000 to 1750 m.

Of the 20 *T. binghami* females (40.5 - 293.5 mm) from bottom trawls, 18 were caught on the continental slope at depths between 1270 and 2193 m, one at 1100 m, and a single specimen from the central Gulf of Mexico at 3151 to 3200 m. The single, metamorphosed male was caught together with one of the females at 1938 m.

Both specimens of *T. axeli* were caught at abyssal depths of 3570 and 3595-3695 m, respectively. Finally, the holotype of *T. pagidostomus* was obtained at 1440 m.

Thus, it appears that the young larvae of *Thaumatichthys* are epipelagic as those of other ceratioids. The older larvae and youngest metamorphosed females are meso- and bathypelagic, and at a length of 40 to 50 mm they become benthic in contrast to all other known ceratioids. Most *T. binghami* and the only known *T. pagidostomus* are caught on the continental slope in bathyal depths of between 1000 and 2000 m, while both specimens of *T. axeli* were obtained in abyssal depths of about 3600 m.

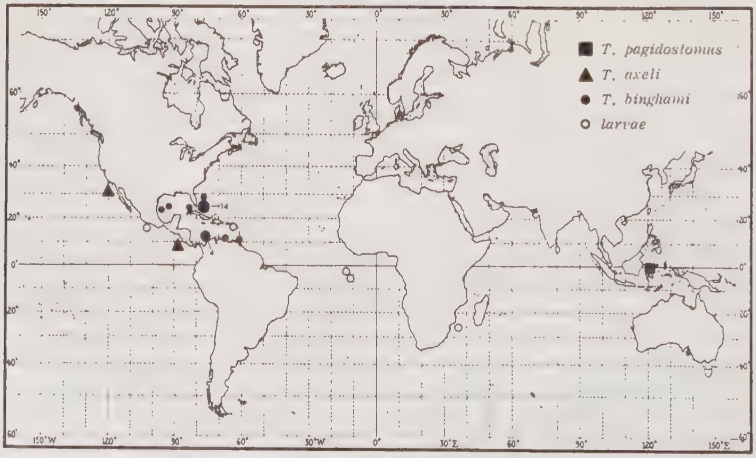

Fig. 16. Known distribution of *Thaumatichthys* species.

IV. BIOLOGY AND FUNCTION OF JAW MECHANISM

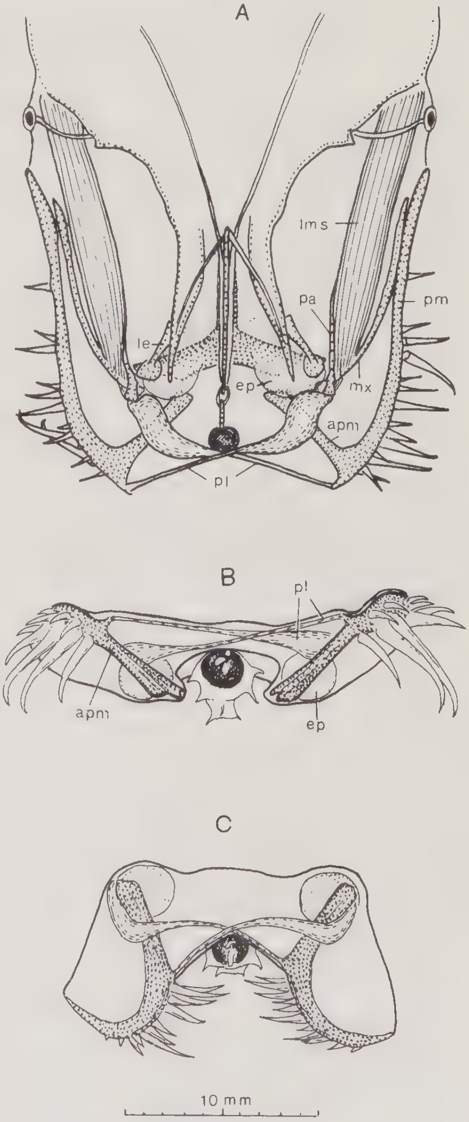

Fig. 17. Jaw mechanism of *Thaumatichthys binghami.* A, dorsal view; B and C, anterior views; A and B, open; C, closed. (apm: articular process of premaxillary, ep: projection of ethmoid cartilage, lms: levator maxillae superioris, pl: premaxillary ligaments; other abbreviations as in Fig. 1).

In his description of *Galatheathauma axeli,* Bruun (1953, 1956) assumed that adolescent and adult *Thaumatichthys* might be benthic. He wrote: "There is a possibility that our fish was caught as the trawl was on its way up; but if that were so, it is strange that it had never been caught before. It seems to me to be far more probable that we here have a deep-sea angler-fish which lives close to the bottom. There it need only lie with its jaw open, leaving the large light organ ... to lure the fish or prawn to it; ..." This assumption has now been supported by the numerous records of specimens caught in bottom trawls and by the continued lack of catches in pelagic nets except for larvae and juveniles. Furthermore, as discussed below, several features in the morphology of *Thaumatichthys* may be regarded as adaptations to benthic life. As a final proof of the correctness of this assumption, stomach contents of unquestionable benthic origin was found in one of the specimens here described.

Most of the specimens were examined for stomach contents, but, except for the largest specimen of *T. binghami,* they were all empty. The stomach of this individual contained three well preserved specimens (50-80 mm long) of the holothurian *Benthodytes typica.* According to Bent Hansen (Zool. Mus., Copenhagen), who has kindly identified the specimens, this species occurs in abyssal and bathyal depths. Its anatomy suggests that it is benthic. A piece of dead sargasso weed and some undeterminable plant remnants were found imbedded between the holothurians.

The extraordinary jaw mechanism of *Thaumatichthys* has been commented on by several authors. Smith & Radcliffe (1912) named the first known specimen *pagidostomus,* i.e. "trap-mouth", and wrote "It would appear that the cavernous, elastic mouth is a trap into which the food is lured and dispatched". Regan (1926) pictured the similar jaw mechanism of *Lasiognathus saccostoma* with opened and closed premaxillaries, and wrote " ... the prey, which is evidently enclosed by the downward movement of the premaxillaries, the bristle-like teeth being used not for piercing, but to close the aperture of the pouch", and Bruun (1956) called the *Galathea* specimen "a living 'mouse-trap' with bait".

The main element of this mechanism is shown in Fig. 17. The anterior tip of each premaxillary is connected with the head of the maxillary and of the palatine of the opposite side by a very elastic ligament (here termed "the premaxillary ligaments"). The two ligaments cross each other in front of the esca. Their more slender distal parts in front of this crossing support the edge of the membrane connecting the premaxillaries; posteriorly they are club-shaped and inflated and pass over the long articular processes of the premaxillaries. The premaxillary processes, which are loosely attached to the maxillaries by ligaments, are able to rotate on the semispherical projections of the ethmoid cartilage. In relation to the longitudinal axis of the head, the premaxillaries are rotated nearly 180° when they are moved from the open to the closed position. The articular processes of the premaxillaries point obliquely down and inwards when the jaws are lifted, and up and outwards when they are lowered. In both positions the elastic premaxillary ligaments pull the tips of the premaxillaries towards each other, thus contributing to the opening as well as the closing of the mechanism. This can be observed directly on the preserved specimens in which the ligaments are still very elastic. When the premaxillaries are pushed from the open position in which they are usually preserved, the ligaments are stretched until a certain intermediate position is reached, and will then snap the jaws together into the closed position.

However, the long and extremely well developed upper jaw muscles (levator maxillae superioris) which posteriorly are inserted on the hyomandibulars and anteriorly on the anterior end of the maxillaries, form the main "spring" of the "trap". Their contraction will cause a back and slightly outwardly directed pull on the maxillaries which, directed by the cartilages and ligaments, is transferred into an up and outward pull in the articular processes of the premaxillaries in such a way that these long processes, like a pair of handles, will turn the jaws downwards into the closed position. As no muscles are present which can account for the lifting of the premaxillaries, it must be assumed that the relapse into this position is accomplished by the elastic ligaments, bones, and cartilages of the mechanism when the levator muscles are relaxed.

This highly specialized jaw mechanism permits the upper and lower jaw to function independently. With the premaxillaries in open position ready for catch, the lower jaw will be able to open and close in connection with the respiration, and a prey trapped by the long teeth of the closed premaxillaries can be transported further into the mouth within reach of the pharyngeal teeth by movements of the lower jaw.

By means of the extensor and flexor muscles of the illicium, the esca can be raised to a more exposed position under, or in juveniles in front of, the incurved anterior edge of the membrane connecting the premaxillaries, and inclined down and backwards toward the roof of the mouth. Possibly the main function of these muscles is to produce a vibrating movement of the lure.

When the premaxillaries are closed, the esca is completely hidden and protected (Fig. 17 and Plate 2), with the possible exception of the greatly prolonged median appendage of certain specimens (Figs 10 and 12).

According to their positions, the eyes, olfactory organs, and the enlarged sensory papillae on the head are adapted to detecting prey or enemies near the sea floor. The small eyes on the edge of the depressed head will be able to scan the bottom close to the jaws. Most probably they function merely as light detectors because the lens, as in other female ceratioids, is situated close to the retina and probably cannot produce clear images (Munk 1966). This seems to exclude the possibility that the light from the esca can be used directly in search of food. The downward directed nasal papillae and enlarged sensory papillae of the subopercular series, as well as the enlarged papillae on the roof of the mouth, are in an optimal position for the detection and examination of prey on the sea floor.

The fact that the only known stomach contents of a *Thaumatichthys* consists of holothurians (which might not be expected to be attracted by light) as well as of quite large plant remnants, confirms the impression obtained through examination of the food of other ceratioids (Bertelsen 1951, Pietsch 1974, Nolan & Rosenblatt 1975) that, in spite of their highly specialized feeding mechanisms, these fishes tend to be omnivorous. By means of these mechanisms, they are enabled to catch otherwise difficultly obtained prey, but they will swallow anything that might serve as food.

V. CLASSIFICATION AND RELATIONSHIPS

with a comparative description of the osteology of *Lasiognathus*

The family Thaumatichthyidae was erected by Smith & Radcliffe (1912) in connection with their description of its first known species, *T. pagidostomus*. They distinguished the family from "the Ceratiidae" which, at that time, included all other known genera of ceratioids, "by the greatly expanded and depressed head, the slender body, the shape of the upper jaw, the dentition, the absence of free dorsal spines, the remarkable modification of the illicium, etc."

In connection with the preliminary descriptions of new genera and species of ceratioid fishes, Regan (1925) divided the suborder into six families. In one of the new families, the Oneirodidae, he placed *Oneirodes* Lütken, 1871, *Dolopichthys* Garman, 1899, *Lophodolus* Lloyd, 1909, and a new genus, *Lasiognathus*, which he defined (l.c.) as "Near *Dolopichthys*, but upper jaw projecting far in advance of lower, and premaxillaries connected with head by a wide membrane, which permits them to meet anteriorly either above the snout or below it". *Thaumatichthys* Smith & Radcliffe, 1912, is not mentioned in this paper, but in Regan's more detailed revision of the suborder Ceratioidea (Regan 1926), it is included in the Oneirodidae with the definition "Resembles *Lasiognathus* in structure of mouth, but is generically distinguished by the shorter head, the dentition, the illicium, and the spinate skin of the lower half of the fish". Regan & Trewavas (1932) kept *Lasiognathus* and *Thaumatichthys* in the Oneirodidae and erected for *T. binghami* Parr, 1927, a new genus *Amacrodon* based on its apparent great difference from *Thaumatichthys* in dentition. Bruun (1953) did not state directly his reasons for placing *Galatheathauma axeli* in a new genus separate from *Thaumatichthys.* Whitley (1970) erected a new family, Galatheathaumatidae, for this species, solely based on the statement that "it differs from other families of angler-fishes in having the luminous lure forked and hanging down from the palate inside the mouth". No reference was made by Whitley to *Thaumatichthys* or *Amacrodon.*

Pietsch (1972) resurrected the family Thaumatichthyidae Smith & Radcliffe, 1912, to include *Lasiognathus* Regan, 1925, *Thaumatichthys* Smith & Radcliffe, 1912, and *Amacrodon* Regan & Trewavas, 1932 *(Galatheathauma* Bruun, 1953, is not mentioned). He states (l.c.) that "... these genera possess several important and unique characters that justify familial status", but no characters other than the projecting upper jaw and the presence of denticles on the esca are mentioned.

As will appear from the preceding description of the individual and ontogenetic variations observed in the now known specimens, none of the differences between *Thaumatichthys* and the type species of the two genera *Amacrodon* and *Galatheathauma* are of an order which justifies a separation on generic level, for which reason they are here synonymized.

To evaluate the justification of placing *Thaumatichthys* and *Lasiognathus* in a family separate from the Oneirodidae, it is necessary to consider the characters which are common to these two genera as well as those which link *Lasiognathus* to the oneirodids. For this reason the osteology of a specimen of *Lasiognathus* was examined*. As the main features of its osteology will appear directly from the illustrations (Fig. 18), and as a complete description would be outside the scope of this paper, only those details will be considered here which seem relevant to the discussion of its relationships.

The three characters which are common to these two genera and distinguish them from all other ceratioids will be discussed first:

1) The jaws. In contrast to all other ceratioids, the premaxillaries of *Thaumatichthys* and *Lasiognathus* are extended far beyond the lower jaw, carry long, hooked teeth, are anteriorly separated and connected only by a membrane, and can be turned upwards and downwards (in the latter position enclosing the lower jaw). In both genera the upper jaw is posteriorly connected to the dentary by means of thin ligaments instead of the solid labial cartilage which, according to Pietsch (1972, 1974), is found in all members of the Oneirodidae.

However, in a number of details this jaw mechanism is differently developed in the two genera.

In contrast to *Thaumatichthys,* the articular processes of the premaxillaries of *Lasiognathus* are relatively short and do not reach the ethmoid cartilage but are attached to anterolateral projections of a well developed, anteriorly notched symphysial

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* This 40.1 mm specimen (SIO 73-305) is recorded by Nolan & Rosenblatt (1975) and kindly presented to the ZMUC. As it lacks esca no specific identification is possible.

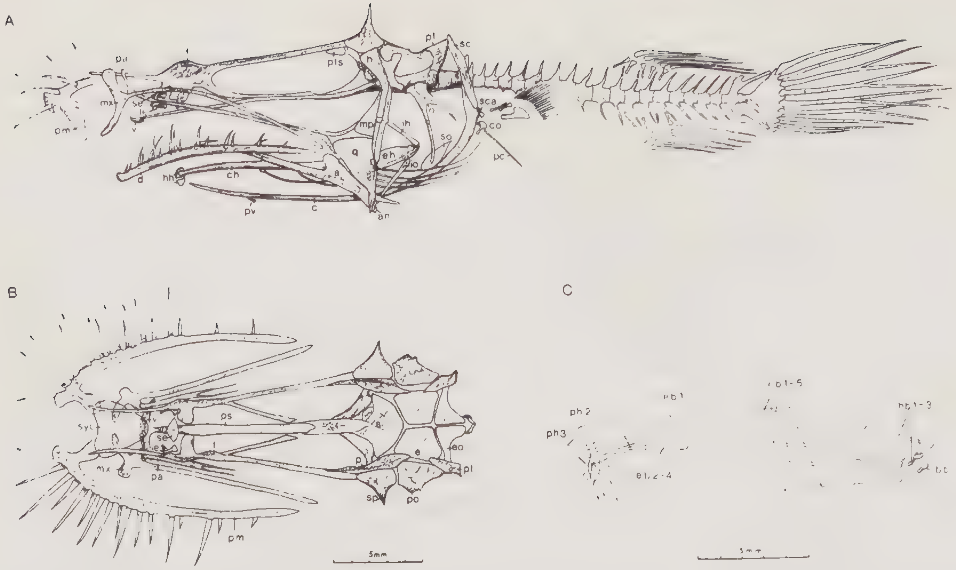

Fig. 18. Skeleton of *Lasiognathus* sp., 40.1 mm (SIO 73-305). A, lateral view; B, dorsal view of head; C, branchial arches. (syc: symphysial cartilage; other abbreviations as in Figs 1 and 5).

cartilage (syc in Fig. 18). This cartilage is present in all oneirodids (Pietsch 1974), but absent in *Thaumatichthys* (cf. p. 9). As in the oneirodids, the posterior end of this cartilage slides on the anterior, slightly concave dorsal surface of the ethmoid cartilage. Furthermore, the dorsal as well as the ventromedial processes of the head of the maxillaries are extremely large and prolonged and clasp the lateral sides of the symphysial cartilage. The levator maxillae superioris muscles are shorter and are attached by a slender ligament to the ventromedial process of the head of the maxillae, rather than behind this head as in *Thaumatichthys*. No premaxillary ligaments are developed (cf. p. 29-30).

The premaxillary teeth of *Lasiognathus* tend to be grouped in oblique series (of 1+1+2+3+3+2+2+1 in left side of the examined specimens), with the anteromediad teeth increasing in length as in *Thaumatichthys*, but the arrangement in regular longitudinal series found in this genus is not distinctly developed.

2) The esca denticles. In most of the genera of ceratioids which have spines in the skin *(Himantolophus, Ceratias, Gigantactis,* etc.), similar dermal spines may be present on the stem of illicium and base of esca, but only *Thaumatichthys* and *Lasiognathus* carry specially developed and arranged denticles on, or imbedded in the distal part of esca.

However, from the descriptions and personal examination of the esca denticles of the holotype of *Lasiognathus saccostoma* and the three specimens of this genus described by Maul (1961, 1962) it appears that, besides in numbers (3), they differ from that of *Thaumatichthys* in shape, colour and position. While the latter is compact and pointed at both ends, transparent and deeply imbedded in the tissues of esca, those of *Lasiognathus* are darkly coloured and have a broad and hollow conical base which is attached superficially in the skin of esca, and thus seems much more similar to skin spines than the *Thaumatichthys* denticle. Additionally, in the *Lasiognathus* species the esca denticles are either borne directly on the esca, or on a filament arising from the esca bulb (Nolan & Rosenblatt 1975).

3) The branching of operculum. In contrast to all other ceratioids, the upper branch of operculum in *Thaumatichthys* and *Lasiognathus* is divided into two or more branches. A more or less broadly expanded upper branch of the operculum with supporting ribs is found in certain oneirodid

genera (e.g. *Chaenophryne* and *Danaphryne),* but in no case with the posterior end divided into two or more points.

The operculum in *Thaumatichthys* is split up into a total of 5-13 radiating rays, including those which seem derived from the lower expanded branch. In *Lasiognathus,* the lower branch of the bifurcated operculum is slender and undivided, while the upper branch is expanded, and in all examined specimens more or less distinctly divided into two by supporting ribs and a low incurvation of its posterior margin. The upper operculum branch may carry a third point as shown in the left operculum of one of the specimens described by Maul (1961). We have examined the small holotype of *Lasiognathus beebi* (USNM 170956) and found it in poor condition. The left operculum figured by Gregory (1933:403), is shriveled and deformed. The three rays of the upper branch of the right operculum are actually ridges, and the shape of the operculum more closely resembles that of the dashed line in Gregory's drawing (see also Bertelsen 1951).

From this it will appear that, in spite of the similarities, these three characters differ significantly in a number of details in the two genera. Especially in possessing a symphysial cartilage and in the shape of operculum, *Lasiognathus* is less distinct from other ceratioids and more similar to the Oneirodidae than *Thaumatichthys.*

Furthermore, *Lasiognathus* differs from *Thaumatichthys* and shows similarities to Oneirodidae in the following characters:

1) a normally developed supraethmoid is present (Fig. 18B)
2) the frontals are anteriorly notched, each with a straight, anteriorly directed slender branch and a ventromedial curved shorter branch; behind the anterior branches each frontal has two ventromedial extensions which contact the parasphenoid; the anterior is short and broad, the posterior long and slender; posteriorly the frontals are widely separated and extremely narrow (Fig. 18A and B)
3) the anterior ends of the parietals overlap the posterior part of the frontals (Fig. 18B)
4) the sphenotics are large (Fig. 18A and B)
5) a small anterior extension of the pterotic overlaps the posterolateral surface of the sphenotic (Fig. 18A and B)
6) the epiotics are closely adjoined behind the supraoccipital (Fig. 18B)
7) the first epibranchials are present (Fig. 18C)
8) the illicium is carried in normal position by a very long pterygiophore, which slides in a deep groove in the upper surface of the skull and between the dorsal muscles of the anterior part of the body
9) the third pectoral radial is much larger than the second (Fig. 18A)
10) the pelvic bones are close set and not posteriorly connected by cartilage
11) the posterior margin of the hypural plate is unnotched (Fig. 18A)
12) the skin lacks spines
13) none of the adaptations to benthic life observed in *Thaumatichthys,* i.e., the depressed shape of head and anterior part of body, the ventrad displacement of eyes and olfactory organs, and the special development of downward oriented, enlarged sensory papillae, are present.

As the male of *Lasiognathus* is unknown, no comparison with characters observed in the male of *Thaumatichthys* is possible. However, this male shows some differences from oneirodids, additional to those observed in the females:

1) the upper denticles are few (4), symmetrically arranged and not fused at base (in oneirodids five to more than twenty, irregularly arranged and emerging from a common bony plate)
2) they are carried by the head of the unresorbed premaxillary (in oneirodid males, the premaxillaries are nearly completely resorbed).

Pietsch (1974) illustrated the phenetic relationships of nine oneirodid genera in the form of a dendrogram based on an analysis of 28 osteological characters each of which were divided into primitive and derived states according to their occurrence in all ceratioids. If the same characters of *Lasiognathus* are evaluated and treated in the same manner, the genus fits into the dendrogram, and would represent a branch close to that of the genus *Dolopichthys.*

The close relationship with oneirodids which, in contrast to *Thaumatichthys,* is found in *Lasiognathus,* and the fact that the two genera show quite noticeable differences even in details of the characters they share might raise the question whether they might be of different descent, and that their similarities might be explained as convergent adaptations. This, however, is hardly probable as it is strongly contradicted by the fact that the three characters which they share and which distinguish them from all other ceratioids seems mutually independent; i.e., the development of denticles on esca as well as the branching of operculum can hardly be supposed to be connected with the specialization of the jaw mechanism.

Most of the characters in which *Thaumatichthys* differs from *Lasiognathus* might be explained as direct results of its unique specialization towards benthic life. The change in shape of head and the displacement of illicium and reduction of its pterygiophore might have led to the change in shape of frontals and in jaw mechanism, which again might have led to the loss of the symphysial cartilage and supraethmoid. It seems more difficult to explain the presence in *Thaumatichthys* of a deep posterior notch in the hypural plate which, according to Pietsch (1972, 1974), is absent in all oneirodids and should be regarded as a primitive character. Possibly the reestablishment of this notch might be caused by some change in the function of the caudal fin in connection with the returning to benthic swimming.

Thus, it becomes a subjective choice whether the genera *Lasiognathus* and *Thaumatichthys* both should be included in the Oneirodidae as Regan (1926) did, or placed together in Thaumatichthyidae as proposed by Pietsch (1972), or whether each of them should be referred to a family of its own. The differences between the two genera seem in fact to be of a similar order as those which separate *Lasiognathus* from oneirodids, and as those which are used for the separation of several of the six ceratioid families which are based on a single genus each. However, to avoid superfluous alterations we prefer to retain Thaumatichthyidae Smith & Radcliffe in the enlarged sense proposed by Pietsch.

The separation to species promulgated here of the known specimens of *Thaumatichthys* is in accordance with their distribution. The specimens from the western North Atlantic area are all referred to *T. binghami*. As the esca is badly preserved in the holotype and only known specimen of *T. pagidostomus* from near Sulawesi (Celebes), the only observed characters which distinguish *T. binghami* from this species are small but, according to the observed intraspecific variations, significant differences in length of certain premaxillary teeth (p. 18), in relative length of the premaxillary bone (p. 11), and relative size of skin spines (p. 24). The holotype of *T. axeli* and the only other metamorphosed specimen from the eastern Pacific were found to differ from *T. binghami* only in certain esca characters (p. 22). In the characters which distinguish *T. pagidostomus* from those referred to *T. binghami* they are similar to the latter.

As shown (p. 21), considerable differences were observed in the number and development of the different appendages of the esca in species of *Thaumatichthys*. The most conspicuous is the development of the second of the two medium appendages which, in some specimens, is developed into a large wormlike organ, a small digitiform in others, and nearly completely absent in the two largest Caribbean specimens as well as in the large holotype of *T. axeli*. If the different developments of this appendage represent specific differences, the Caribbean material should, besides *T. binghami*, include one or two new species (two of which were collected within a few kilometers of each other) and, furthermore, the smaller Pacific specimen referred to *T. axeli* should represent a distinct species. Such a separation seems most unlikely, and is in no way supported by a comparative examination of measurements and counts.

On the basis of the available material, it is more reasonable to conclude 1) that the intraspecific variation in the esca appendages is somewhat larger in *Thaumatichthys* than usually assumed in the ceratioids; 2) that the enlargement of the second median appendage of the *Thaumatichthys* esca starts at a somewhat different size or age of individuals; 3) that this fragile, wormlike part of the "bait", which is left unprotected when the upper jaws are closed, is exposed to attack from predators and is normally lost in older individuals.

VI. TAXONOMY

Family **THAUMATICHTHYIDAE**
Smith & Radcliffe, 1912.

Thaumatichthyidae Smith & Radcliffe, 1912.

Thaumatichthyidae (to include *Thaumatichthys, Lasiognathus,* and *Amacrodon*): Pietsch 1972; Brewer 1973; Nolan & Rosenblatt 1975.

Oneirodidae (in part): Regan 1925, 1926; Regan & Trewavas 1932; Bertelsen 1951.

Galatheathaumatidae (separate for *Galatheathauma*) Whitley, 1970.

Type genus: *Thaumatichthys* Smith & Radcliffe, 1912.

Females: The family Thaumatichthyidae is related to Oneirodidae but distinguished from this and all other families of the suborder Ceratioidei in each of the following characters: premaxillaries extending far beyond the lower jaw, anteriorly separated, only connected by an elastic wide membrane; 1-3 denticles on esca; upper arm of operculum divided into two or more branches. Furthermore, it differs from all other families in the following combination of characters: parietals present; pterosphenoids present; hyomandibular with double head; quadrate spine well developed; two hypurals; six branchiostegal rays; epi- and ceratobranchial teeth absent; three pectoral radials; pelvic bones rod-shaped, slightly expanded distally; illicium and escal light organ present; second cephalic ray rudimentary, labial cartilage absent.

Males and larvae only known in *Thaumatichthys,* cf. this genus.

Key to the genera of THAUMATICHTHYIDAE (females)

1 a. Head narrow, illicium and its pterygiophore long, in normal position on head; esca with three denticles; skin naked; D 5, A 5 .... *Lasiognathus*

1 b. Head broad, depressed; illicium and its pterygiophore short; esca sessile in roof of mouth, with one denticle; skin of lower part of head and body spiny; D 6-7, A 4 ...... *Thaumatichthys*

Further diagnostic characters of the genus *Lasiognathus* will appear from the following diagnosis for *Thaumatichthys.* For synonymy and key to the species of *Lasiognathus,* cf. Nolan & Rosenblatt (1975).

Genus ***Thaumatichthys*** Smith & Radcliffe, 1912

Thaumatichthys Smith & Radcliffe, 1912; Regan 1926; Parr 1927; Regan & Trewavas 1932; Bertelsen 1951; Pietsch 1972; Brewer 1973.

Amacrodon Regan & Trewavas, 1932; Parr 1934; Bertelsen 1951; Pietsch 1972.

Galatheathauma Bruun, 1953; Bruun 1956; Wolff 1960, 1961; Whitley 1970.

Type species: *Thaumatichthys pagidostomus* Smith & Radcliffe, 1912.

Females of the genus *Thaumatichthys* are distinguished from the only other genus of the family as well as from all other known ceratioid fishes in being benthic, having the esca sessile in the roof of the mouth and with a deeply imbedded single curved denticle, depressed head with eyes and olfactory papillae posteroventrad displaced to the corner of the mouth, and operculum divided into 6-13 radiating rays.

Furthermore, it differs from *Lasiognathus* in the following characters: symphysial cartilage absent; supraethmoid absent in juveniles, incompletely developed in adults; frontals anteriorly unnotched and lacking posterior ventromedial extensions; sphenotic small with short spine; head of maxillary with short processes; first epibranchials absent; second and third pectoral ray of nearly equal size, fusing with age; pelvic bones widely spaced, distally connected by a band of cartilage; hypural plate with a deep posterior notch; six to seven dorsal and four anal fin rays; pterygiophore of illicium short, completely hidden under skin of head; esca with one to three pairs of lateral, pointed lobes, in larger specimens prolonged into tapering tentaclelike filaments and two median appendages, the posterior one pigmented and, in certain stages, greatly prolonged; enlarged sensory papillae under eye and anteriorly in roof of mouth; skin with spines on lower part of head and body.

Thaumatichthys males differ from all other known ceratioid males in the development and position of the denticles on the snout. They have toothless but otherwise unresorbed premaxillaries carrying at tip 4 separate denticles arranged in two pairs above each other; the lower pair shorter and more strongly hooked than the upper; on tip of lower jaw 7 denticles, fused at base and arranged in a lower transverse series of 4 and an upper of 3 which are shorter and more hooked than in the lower series. Furthermore, they are distinct from all other ceratioids in having operculum divided into several (7-13) radiating rays, and from *Lasiognathus* in lacking supraethmoid and in having 6-7 dorsal, 4 anal fin rays and spiny skin.

Thaumatichthys larvae differ from all other ceratioid larvae in having a layer of subdermal melanophores covering the whole surface of the head and body, and, furthermore, from *Lasiognathus* in number of dorsal and anal fin rays.

Key to the species of THAUMATICHTHYS (females)

1 a. Length of premaxillary 33% s.l. Anterior premaxillary teeth long: I 1:3.8, II 1:3.0, II 2:6.5, II 3:7.0, III 2:3.3, III 3:4.3, IV 2:2.4 and V 2:3.4 mm .... *pagidostomus* (off Sulawesi)
1 b. Length of premaxillary 23.5%-27.0% (average 25.4%) s.l. (in specimens of 40 mm and more). Anterior premaxillary teeth somewhat shorter: I 1:2.2-3.5, II 1:1.1-2.3, II 2:3.0-5.6, II 3:3.8-5.8, III 2:0.8-2.3, III 3:1.8-3.4, IV 1:0.9-2.3 and V 2:0.8-2.6 mm 2
2 a. Esca with two or three pairs of lateral pointed lobes which in larger specimens are prolonged into tapering tentaclelike filaments; the uppermost median appendage of esca digitiform and tapering .... *binghami* (Caribbean and adjacent waters)
2 b. Esca with a single pair of lateral pointed lobes which in larger specimens are prolonged into tapering tentaclelike filaments; the uppermost median appendage of esca wartlike and untapering .... *axeli* (tropical eastern Pacific)

Thaumatichthys pagidostomus
Smith & Radcliffe, 1912
(Figs 3, 7, 8, 13, 16)

Thaumatichthys pagidostomus Smith & Radcliffe, 1912, p. 580-581; Regan 1926, p. 31; Parr 1927, p. 24; Regan & Trewavas 1932, p. 91; Bertelsen 1951, p. 121 (in part).

Holotype USNM 72952, a female 60.0 mm s.l. *Albatross* St. 5607, off Sulawesi (Celebes) 00°04'S, 121°36'E, beam trawl at 1440 m, 18 Nov. 1909.

Diagnostic characters in the key.

No other records.

Thaumatichthys binghami
Parr, 1927
(Figs 1, 3-11, 13, 14, 16, 17; Pls 2, 3)

Thaumatichthys binghami Parr, 1927, p. 24-25.
Amacrodon binghami, Regan & Trewavas 1932, p. 91; Parr 1934, p. 7; Bertelsen 1951, p. 122.

Holotype BOC 2015, a female 36.5 mm s.l. *Pawnee* St. 25, 24°51'N, 76°37'W, pelagic net with 8000 feet wire, 17 March 1927.

Diagnostic characters in the key.

Examined material (including the holotype): Seventeen female specimens 36.5-293.5 mm s.l. (cf. App. Table 1), all from the Caribbean and adjacent areas. Three specimens 36.5-45.0 mm caught pelagic in intermediate depths, the other 14 specimens, 40.5-293.5 mm, in bottom trawls at 1100-3200 m (cf. p. 29).

After this study was finished we have been informed that in the Tongue-of-the-Ocean Programme of UMML additionally 6 *Thaumatichthys* females, 55.6-134.0 mm, have been obtained, all in semi-balloon trawl at depths from 1387 to 2193 m and inside the area 23°52'-24°46'N, 75°26'-77°22'W. According to information on their esca characters, kindly furnished by Dr. Jon C. Staiger, they represent *T. binghami*.

The metamorphosed male, 31.0 mm (ZMUC P921946) and the male larva, 18.5 mm (*Dana* St. 1186), both from the same area, most probably belong to this species.

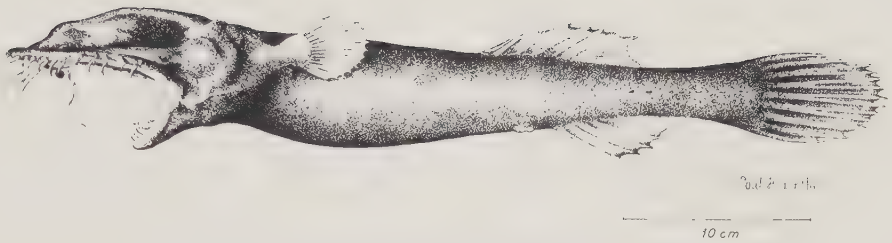

Fig. 19. The holotype of *Thaumatichthys axeli*.

Thaumatichthys axeli
(Bruun, 1953)
(Figs 2, 3, 6, 7, 8, 12, 13, 15, 16, 19; Pl. 1)

Galatheathauma axeli Bruun, 1953, p. 174-177, 1956, p. 174-177; Wolff 1960, p. 175, 1961, p. 137; Munk 1964, p. 10; Whitley 1970, p. 246.

? *Thaumatichthys pagidostomus*, Brewer 1973, p. 25.

Holotype ZMUC P92166, a female 365 mm s.l. (Fig. 19). *Galathea* St. 716, 09°23'N, 87°32'W, in herring otter trawl at 3570 m, 6 May 1952.

Diagnostic characters in the key.

A second female specimen of 85.5 mm, SIO 70-2265, Melville Expedition MV 69-VI, St. 9, 31°19.7'N, 119°39.2'W, in otter trawl at 1968-2019 fathoms (3595-3695 m) depth, 18 Dec. 1969. A female larva of 22.6 mm (LACM 31107-1) from the same eastern Pacific area may belong to this species (Fig. 15).

Thaumatichthys sp.
Thaumatichthys pagidostomus (?) Bertelsen, 1951.

Three larval specimens, one male of 4.4 mm in total length from the Indian Ocean south of Madagascar (*Dana* St. 3964), one male of 6 mm (*Dana* St. 4000), and one female of 10 mm in total length (*Dana* St. 3999) from the equatorial east Atlantic cannot be referred to species.

VII. SUMMARY

This study is based on the 365 mm large holotype of *Thaumatichthys (Galatheathauma) axeli* (Bruun 1953) caught in the east Pacific by the Galathea Expedition, the eight previously known 3-60 mm specimens which are here referred to this genus, and seventeen 40.5-293.5 mm specimens not previously recorded.

A general description of the genus is presented, including the osteology, dentition, jaw mechanism and illicium and esca structures of the females and a description of the previously unknown male.

On this basis the taxonomy of the genus is revised. The genera *Amacrodon* Regan & Trewavas, 1932, and *Galatheathauma* Bruun, 1953, are synonymized with *Thaumatichthys* Smith & Radcliffe, 1912, and it is concluded that the known specimens of this genus represent three species: *T. pagidostomus* Smith & Radcliffe, 1912, *T. binghami* Parr, 1927, and *T. axeli* (Bruun, 1953).

The relationships of *Thaumatichthys* to other genera of Ceratioidea is discussed mainly on the basis of a comparative study of a representative of the genus *Lasiognathus* Regan, 1925, which together with *Thaumatichthys* forms the family Thaumatichthyidae Smith & Radcliffe, 1912, as resurrected by Pietsch (1972). It is shown that besides the characters which the two genera have in common and which separate them from all other ceratioids, *Lasiognathus* differs from *Thaumatichthys* and shows similarities to the family Oneirodidae in a great number of characters. This might warrant the erection of a separate family for the genus *Lasiognathus*, but in order to avoid superfluous alterations we prefer to retain Thaumatichthyidae in the enlarged sense proposed by Pietsch. Diagnosis of the family and keys to its genera and the species of *Thaumatichthys* are provided.

Appendix Table 1. Morphometric and mesteristic characters of the

Species	*axeli* (holotype)	*binghami*	*binghami*	*binghami*	*binghami*	*binghami*	*binghami*	*axeli*	*binghami*
Cat. no.	ZMUC P92166	USNM 214571	UMML 30958	ZMUC 1) P921950	UMML 27594	UMML 30930	USNM 214571	SIO 70-2265	ZMUC 2) P921947
Locality	9°23'N 87°32'W	9°58'N 76°29'W	24°23'N 77°23'W	10°10'N 76°14'W	11°25'N 67°10'W	24°15'N 76°07'W	9°58'N 76°29'W	31°20'N 119°39'W	11°30'N 60°14.5'W
Depth	3680 m	1271 m	1510 m	1100 m	1783- 1866 m	1737 m	1271 m	3700- 3800 m	1464- 1848 m
Total length mm	*438.5*	358.5	286	187.5	139.5	121.5	112.1	*112.2*	88.8
Standard length mm	*365*	293.5	225	142.5	112	95.5	87.1	*85.2*	73.1
No. of dorsal rays	*6*	7	7	7	7	6	7	*7*	7
No. of anal rays	*4*	4	4	4	4	4	4	*4*	4
No. of pectoral rays	*14-14*	15-15	15	15	15	14	15-15	*16-16*	15-15
No. of caudal rays	*9*	9	9	9	9	9	9	*9*	9
No. of vertebrae	*21*	21	..	21	..	..	21	*22*	21
No. of teeth in premaxillary:									
present	*45-43*	35-34	42	30-31	24	22	21	*16*	16
lost	*10-11*	3- 3	3 –						
longest tooth, mm	*21.5*	24.0	15.2	11.3	9.8	8.1	5.0	*4.8*	5.7
No. of teeth in dentary	*39-40*	22	30	31-27	25	20	14	*17*	12
longest tooth, mm	*10.5*	10.3	7.9	5.6	3.8	2.4	2.6	*1.5*	1.5
No. of teeth in									
2. pharyngobr.	*15-17*	..	c16	..	12-11	10-11	..	*8-8*	6-6
3. pharyngobr.	*25-24*	.	c20	..	15-15	13-14	..	*9-9*	7-6
longest tooth, mm	*5.5*	..	c2.5	..	2.3	c2	.	*2.2*	1.6
Measurements in % of standard length:									
Tip of pmx - gill opening	*41*	c46	42.5	c45	40.5	44	45.5	*c35*	33.5
Tip of pmx - praeopercle	*32.4*	32.6	32.5	32.5	33.0	32.5	33.4	*30.6*	31.2
Scull length	*23.3*	29.0	c31	c31.5	28.2	c27	31.4	*27.2*	29.0
Width of head between:									
sphenotics	*19.7*	21.6	20.0	18.5	17.4	17.4	18.1	*18.1*	18.6
posttemporals	*13.8*	17.0	17.8	16.0	13.0	14.7	13.6	*12.0*	14.6
Least width of frontals	*c4*	6.5	7.5	c7	7.4	6.3	c7	*6.3*	6.7
Width between angular spines	*34*	31.8	33.5	31.5	28.5	24.6	28.0	*24.6*	28.0
Sphenot.-posttemp.	*11.6*	c8.5	12.5	12.6	c10.5	11.5	10.9	*12.0*	12.1
Sphenot.-angular spine	*12.3*	c10	13.8	11.8	10.7	11.5	10.1	*10.8*	12.1
Length of upper jaw	*25.6*	23.9	25.5	25.1	25.9	24.6	25.7	*26.5*	25.3
Length of lower jaw	*22.5*	20.1	21.8	20.9	22.4	20.4	20.0	*c21*	19.0
Diameter of eye	*0.7*	0.8	1.1	1.2	c1.8	1.8	1.5	*2.2*	1.9
Length of illicium	*5.8*	6.1	c6.5	6.0	c4.5		4.8	*5.8*	c5
Length of basal bone	*13.6*	c15		c14	15.8		15.0	*14.1*	13.1
Diam. of esca gland	*2.5*	2.7	3.8	3.5	3.2	3.0	3.0	*2.9*	2.6
Depth of body		c10	c13	c7.5	c10	c9.5	c8.5		
Least depth of caudal peduncle	*c7*	6.1	8.0	c7	6.6	6.8	c7		
Predorsal length	*61.0*	c67	62.0	c71	62.0	63.0	62.5	*62.0*	62.0
Preanal length	*72.0*	c85	77.0	81	78.0	78.0	81	*73.5*	76.0
Longest ray of:									
caudal fin	*20.1*	32.2	27.2	31.5	24.5	27.2	28.5	*31.6*	21.5
dorsal fin		9.5	14.1	16.5	c13.5		10.9	*17.2*	14.8
anal fin	*c11.5*	6.2	10.4	11.2	c10		9.8	*12.7*	14.8
pectoral fin	*8.5*	8.5	11.6	9.8	c9	c12.5	10.9	*c9.5*	10.5

1) Gift from National Fisheries Service, Pascagola, now deposited in ZMUC.

2) Gifts from UMML, now deposited in ZMUC.

Thaumatichthys species (*T. axeli* and *T. pagidostomus* in italics)

binghami	*binghami*	*pagidost.* (holotype)	*binghami*	*binghami*	*binghami*	*binghami*	*binghami*	*binghami*	*binghami*	*binghami* (holotype)	sp. (larva)
ZMUC 2)	UMML	USNM	UMML	UMML	USNM	UMML	Texas Univ.	UMML	BOC	BOC	LACM
P921948	30926	72952	26927	31362	214570	31363	69-A-11-91	30866	3713	2015	31107-1
[illegible]	24°20'N	00°04'S	23°33'N	23°48'N	[illegible]	23°39'N	22°52'N	28°38'N	25°39'N	24°51'N	17°02'N
76°27'W	75°58'W	121°36'E	82°47'W	77°04'W	91°02'W	76°48'W	96°18'W	76°49'W	77°18'W	76°37'W	102°08'W
1270- 1820 m	1682 m	1440 m	1638 1757 m	1366 m	3151- 3200 m	1307- 1324 m	0-1550 m	1290 m	1050 1100 m	8000 f	780 m
							pelagic		pelagic	pelagic	pelagic
89.0	87.0	*78.0*	72.8	75.0	67.5	67.5	61.0	56.0	54.5	50.0	34.1
69.[illegible]	67.[illegible]	*60.0*	57.2	58.0	51.5	50.5	45.0	40.5	40.0	36.5	22.6
7	7	*7*	7	7	7	7	7	7	7	6	7
4	4	*4*	4	4	4	4	4	4	4	4	4
15-15	16	*16-16*	15-15	15	15	15	15	15	15	15	14-14
9	9	*9*	9	9	9	9	9	9	9	9	9
20		*20*	21		21		21		21		21
14	16	*16*	14		13	16	11	15	12	12	
5.8	4.3	*7.0*	4.8		4.3	5.2	3.0	4.5	1.7	1.5	
17	16	*13*	13		12	10	10	9	9	7	
1.9	2.0	*2.0*	1.2		1.5	1.5	1.2	1.2	(0.6)		
8-8	c7	*4-7*	4-4			5-5	4	5-6			
9-10	c10	*8-8*	6-6			7-7	5	7-8			
1.5		*2.0*	1.5			c1.0	1.2	c1.0			
36-37	43		40.0	42.0	40.0	48.5	47.0	43.4	45.0	c44	c40
30.8	33.8	*35.0*	33.8	30.2	31.0	34.5	32.0	c33	25.5		c26.5
26.6	c29	*29.0*	29.1	27.5	27.5	31.5	31.0	c26	28.2		c26.5
19.2	18.2	*17.5*	17.8	19.5	19.4	21.0	20.0	c18.5	19.0	21.8	22.1
15.0	14.5	*13.8*	12.9	14.8	13.2	14.9	15.1		14.7		22.1
7.4	6.3	*7.5*	6.6	6.9	7.8	8.0	6.7	c8	7.3		c17
27.8	27.0	*32.4*	22.7		27.2		28.9		31.3	c23	
12.2	11.4	*10.7*	11.5	c11.5	12.6	13.7	14.9		16.8		c17
12.8	13.2		13.6	14.4		13.9	15.2		15.6	16.5	27.4
24.3	25.0	*32.8*	25.5	26.0	23.4	26.5	26.3	27.0	25.0	17.8	15.5
19.6	21.7	*26.2*	20.4	20.0	21.8	21.8	22.2		19.7	18.2	20.4
2.4	2.2	*2.5*	2.6	3.3	2.3	2.8	3.3	3.0	3.0	4.4	6.2
c5.5			5.9		4.8		5.6		5.7	5.5	3.5
14.3	14.6	*16.5*	13.6	13.8	13.6		16.2	17.8	11.7		14.2
2.1	3.6		2.8	2.6	3.3	3.4	3.7	4.0	3.0	3.3	
	12.4			13.0	13.0	14.3	15.6	c14	18.7	13.1	80
	8.4	*c7.5*		9.1	10.2	9.3	11.6	9.4	13.5	9.3	
62.5	66.0	*64.0*	62.9	60.5	60.0	65.0	c65	c60	60.0	c63	66.3
72.5	77.0	*78.0*	76.3	c80	78.0	80.0	c80	c43	73.0	c71	73.0
27.4	30.0	*c30*	27.2	29.3	31.0	33.6	38.0	38.0	36.3	c33	51.0
14.9	14.3	*c12*	c13	15.6	c18.5		c19	c25	c22.5		38.0
14.3	11.2	*c13*	c13		c14.9		c10		c18.5		31.0
12.3	12.7	*c12*	11.8	c13	14.7	13.5	15.5	16.5	16.7	15.4	23.0

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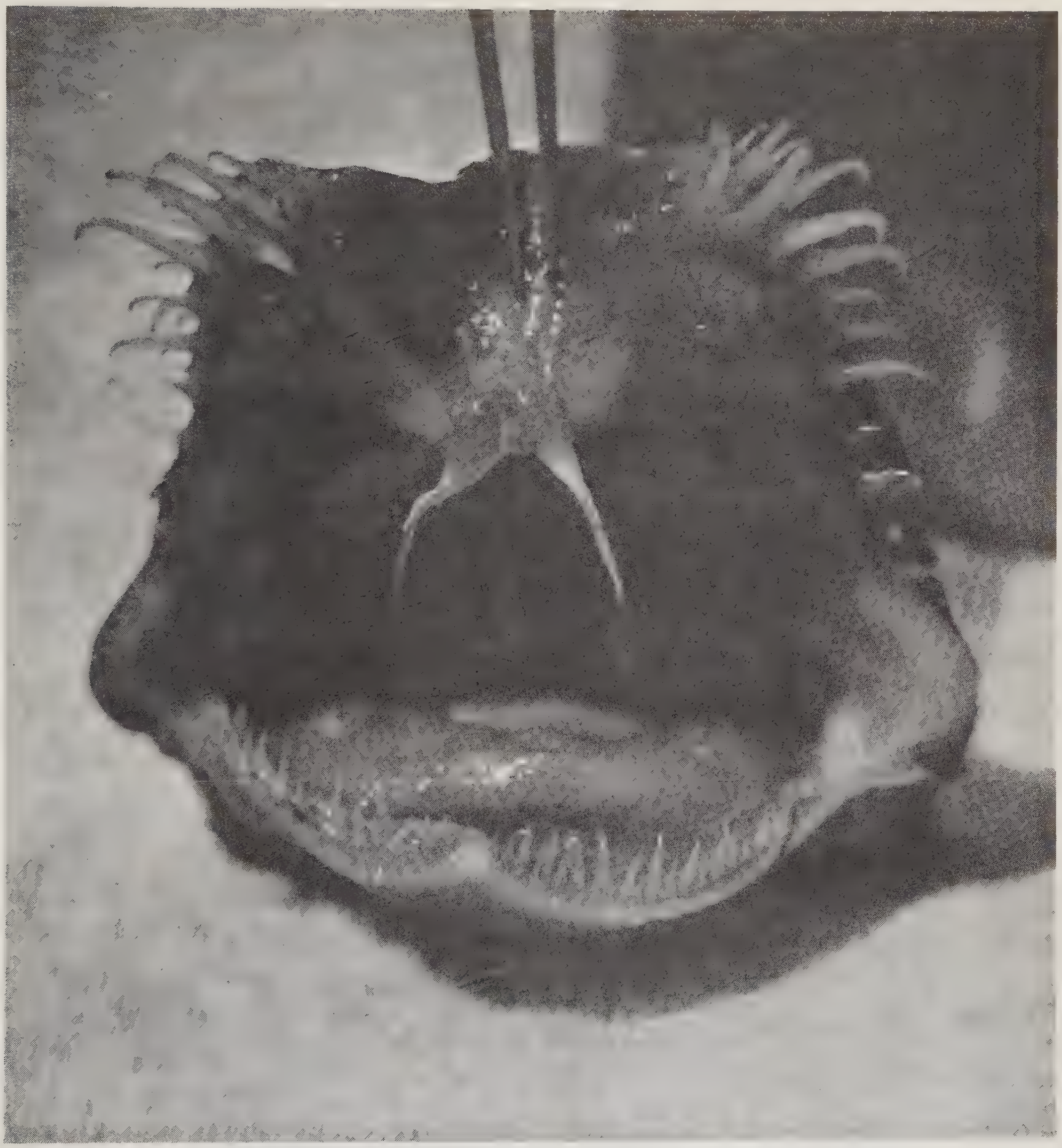

PLATE 1

Thaumatichthys axeli, holotype, photographed onboard the *Galathea* just after the catch.

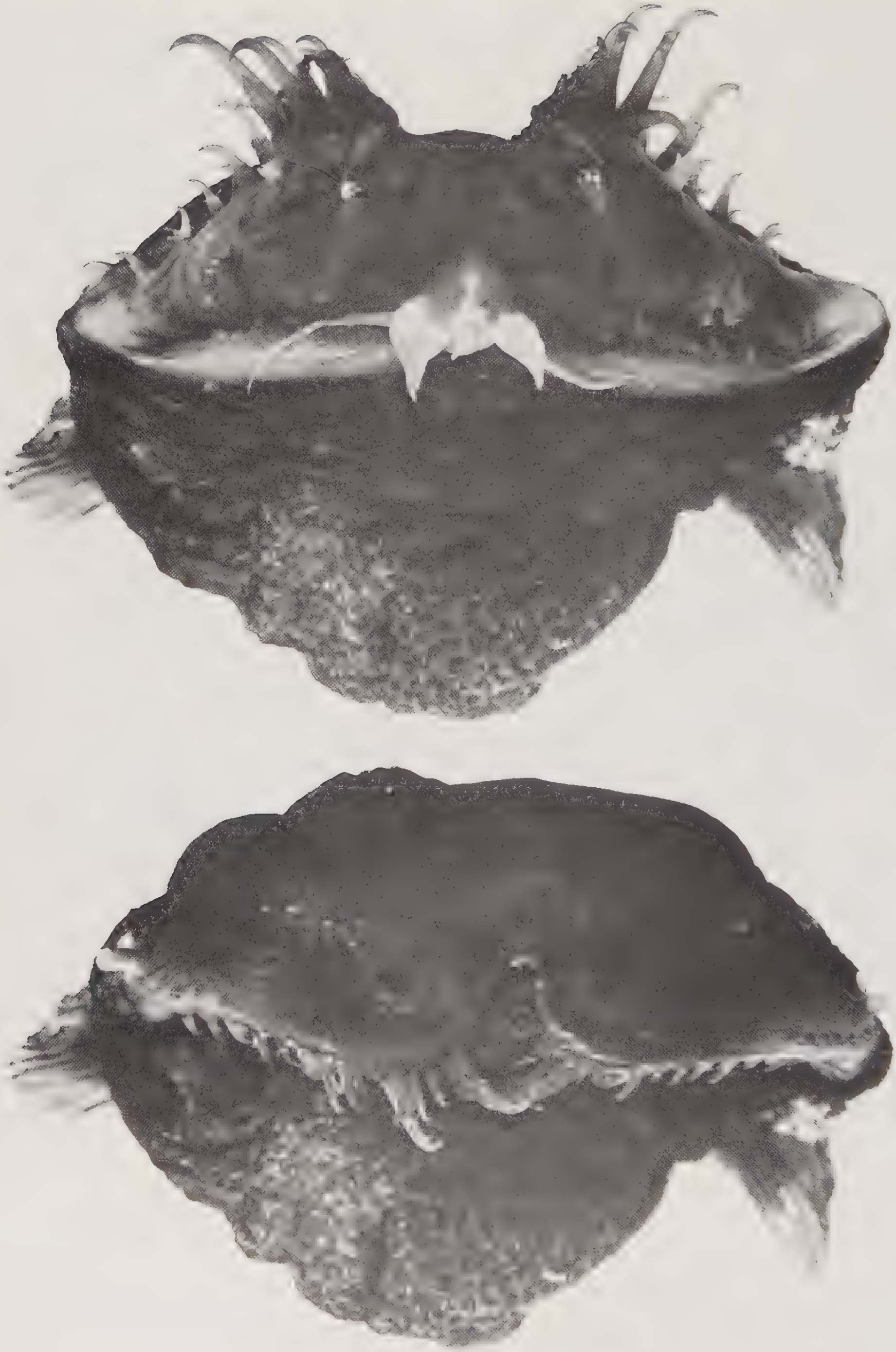

PLATE 2

Thaumatichthys binghami, 225 mm (UMML 30958).

Above: with raised upper jaws and exposed esca. Note also the large sensory papillae in the roof of the mouth.

Below: with closed mouth. Note the position of the eyes and olfactory organs and, below and in front of these, the large lateral line organs of the suborbital series.

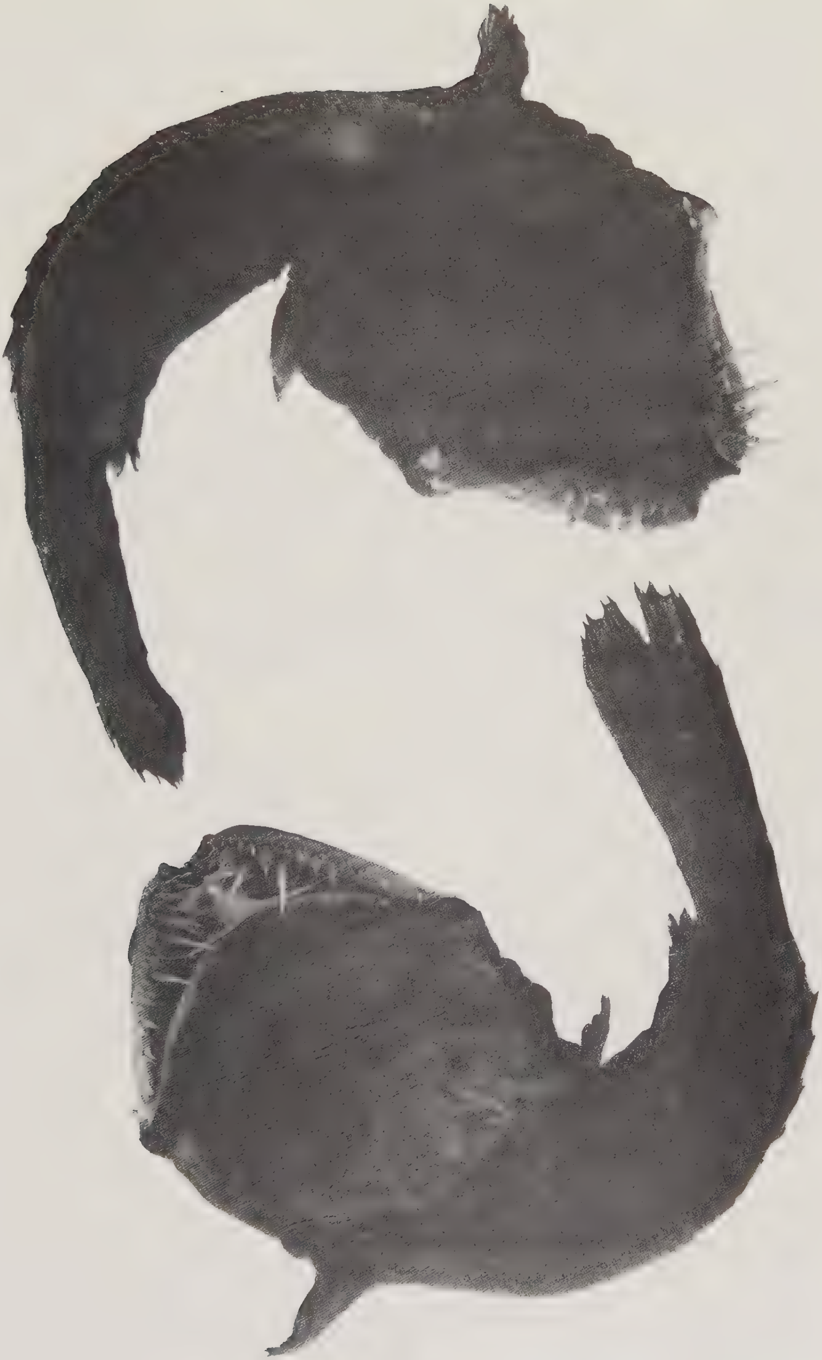

PLATE 3

Thaumatichthys binghami, 225 mm (UMML 30958).

Above: in dorsal view with raised upper jaws.

Below: in ventral view with closed mouth.

7706

Annual Physical and Chemical Oceanographic Cycles of Auke Bay, Southeastern Alaska

HERBERT E. BRUCE, DOUGLAS R. McLAIN, and BRUCE L. WING[1]

ABSTRACT

The annual cycles of physical and chemical oceanographic conditions in Auke Bay, a small estuary in southeastern Alaska, showed a consistent pattern over an 8-yr period (1961-68). The cycles closely followed seasonal climatological and atmospheric events. Increased insolation in the spring caused general warming of the surface water and the air, which in turn increased the freshwater input into Auke Bay from melting snow and ice. The fresh water lowered surface salinities and together with warming of the surface waters caused a density stratification of the water column, which increased as the spring-summer season progressed. Maximum stratification occurred in August, followed by a general decay of stratification in September. Vertical mixing of the top 20 m of the water column by fall storms in September and cooling of surface water resulting from decreased insolation set up a thermohaline circulation that continued through the fall and early winter. The water column became homogeneous by January and remained thoroughly mixed from January through March or early April.

Auke Bay was rich in the inorganic nutrients phosphate, silicate, and nitrate. Spring phytoplankton blooms followed the onset of stratification and drastically reduced the concentration of all three nutrients in the surface water. Nitrate was essentially depleted and remained so throughout the summer. Low nitrate availability was undoubtedly one of the important factors limiting primary production in Auke Bay.

INTRODUCTION

Auke Bay is one of the many small bays along the major straits and passages of the inside waters of southeastern Alaska. Although these bays represent a small percentage of the total water mass of the area, they are important as spawning and nursery grounds for several species of fish and shellfish. Streams tributary to Auke Bay are spawning grounds for four species of salmon: pink, *Oncorhynchus gorbuscha*; chum, *O. keta*; coho, *O. kisutch*; and sockeye, *O. nerka*. Herring, *Clupea harengus pallasi*; king crabs, *Paralithodes camtschatica* and *P. platypus*; snow crab, *Chionoecetes bairdi*; and other species of commercial and recreational value spawn in the bay itself.

Several reports describe aspects of physical and chemical oceanography of small bays and estuaries in southeastern Alaska. Barnes et al. (1956) made an intensive survey (including some biological observations) of Silver Bay on Baranof Island near Sitka before construction of a pulp mill. Powers (1963) examined Little Port Walter at the southern end of Baranof Island. The U.S. Federal Water Pollution Control Administration (1966) made surveys of Gastineau Channel and Fritz Cove near Juneau and of Silver Bay and Ward Cove near Ketchikan in the summer of 1965. McLain (1968) surveyed Traitors Cove on Revillagigedo Island. McLain (1969) described seasonal changes in oceanographic conditions in Lynn Canal. Nebert and Matthews (1972) described the circulation of Endicott Arm. Most of these studies were less than 2-yr duration, not long enough to separate short-term and protracted hydrographic disturbances known to occur in natural environments.

Therefore, in our study of Auke Bay, the objective was to describe the annual cycles of oceanographic conditions in the bay over several years. In this way the complete annual cycle and the range of natural environmental variability could be identified. From this information the biological consequences of normal cycles and anomalous oceanographic conditions could be assessed.

DESCRIPTION OF STUDY AREA

Physiography and Geology

Auke Bay is one of a large number of small embayments off a system of large fiords connecting with the open ocean (Fig. 1). It is located at lat. 58°22′N and long. 134°40′W, 19.3 km northwest of Juneau, Alaska, and about 130 km inland from the open Gulf of Alaska. The bay covers an area of about 11 km^2 and contains several small islands and reefs.

The bottom topography of the bay is irregular, and submarine gulleys and mounts are quite common (Fig.

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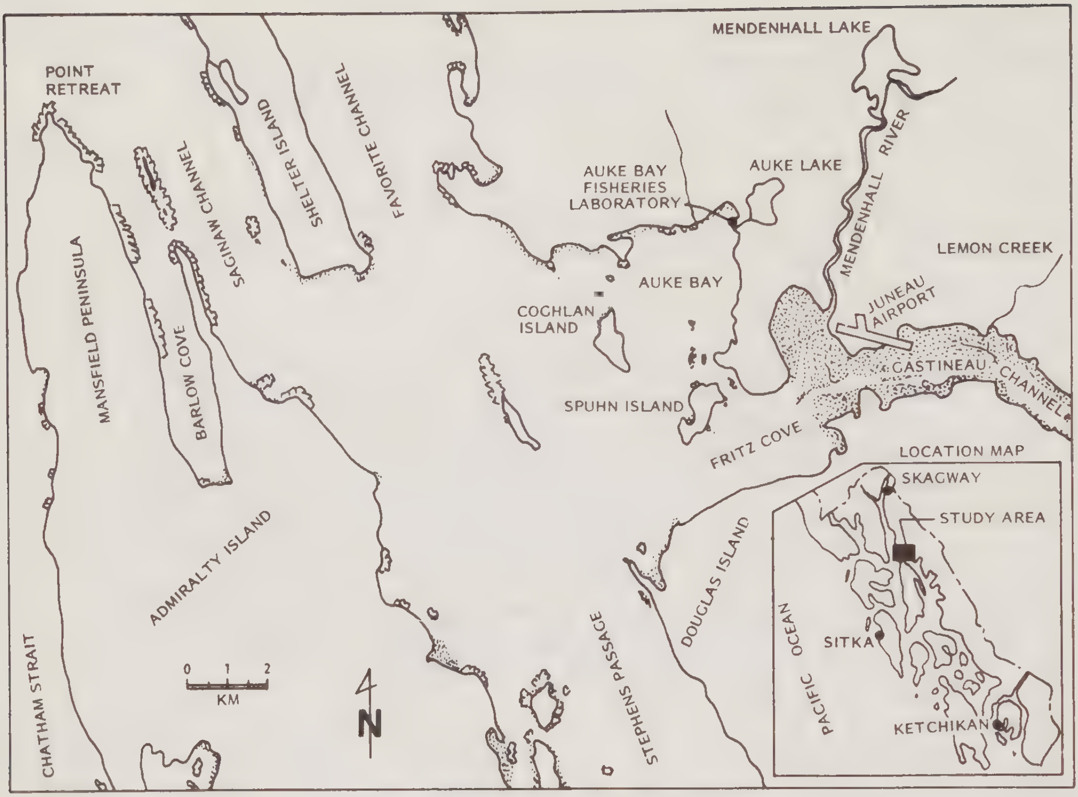
MENDENHALL LAKE
POINT RETREAT
SHELTER ISLAND
FAVORITE CHANNEL
SAGINAW CHANNEL
MENDENHALL RIVER
AUKE BAY FISHERIES LABORATORY
AUKE LAKE
MANSFIELD PENINSULA
LEMON CREEK
AUKE BAY
JUNEAU AIRPORT
COGHLAN ISLAND
BARLOW COVE
GASTINEAU CHANNEL
SPUHN ISLAND
FRITZ COVE
LOCATION MAP
SKAGWAY
STUDY AREA
ADMIRALTY ISLAND
DOUGLAS ISLAND
PACIFIC OCEAN
SITKA
STEPHENS PASSAGE
CHATHAM STRAIT
0 1 2
KM
N
KETCHIKAN

Figure 1.—Auke Bay, Alaska, and surrounding area.

2). The maximum depth, 100 m, is near the south end of Coghlan Island; depths of 40 to 60 m are common over much of the bay.

Auke Bay is not a fiord-type estuary of the form described by Pritchard (1952), but is a small tributary embayment to a system of large fiords. Lynn Canal-Icy Strait-Chatham Strait and Stephens Passage-Frederick Sound-Chatham Strait are major interconnected passages in southeastern Alaska and provide communication between Auke Bay and the Gulf of Alaska. The entire region was heavily glaciated during the Pleistocene Eopch. Martin and Williams (1924) concluded that glacial deepening of a preexisting river valley was the primary process in the formation of the Chatham Strait-Lynn Canal fiord. Auke Bay may have formed as a side valley of the larger fiord system.

Climatology

Auke Bay lies within that part of the maritime province extending along the northwest coast of North America. Winds in this area are predominantly southerly off the Pacific Ocean. These warm, moisture-laden winds strike the high coastal ranges and result in abundant precipitation, little sunshine, and moderate air temperatures. Observations by the National Weather Service at the Juneau Airport 3 km east of Auke Bay are that precipitation in the area is lightest in the spring and heaviest in the fall (Fig. 3). Between February and May the average monthly precipitation rate is fairly constant (the monthly average for 1931-60 was 6.6 cm). Precipitation increases rapidly in June and reaches a maximum in October (the 30-yr average for October 1931-60 was 21.3 cm).[2] After the October maximum, precipitation decreases until February.

The average monthly insolation for the Auke Bay area from 1959 to 1962 is shown in Figure 4. Insolation, which we estimated from cloud cover data, is a predominant factor in controlling seasonal cycles of air and sea surface temperature. Data from Roden (1959) on the total amount of radiation received at sea level under cloudless skies were converted to insolation under cloud cover according to the equation of Sverdrup et al. (1942):

$$Q_1 = Q_0(1\text{-}0.071\ C)$$

where Q_1 = radiation received at sea level adjusted for cloud cover
Q_0 = total incoming radiation under cloudless skies
C = amount of clouds (in tenths of sky covered).

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[2] The average was calculated from data in the U.S. Weather Bureau's annual publication Climatological Data, vols. 17-46, Alaska section (No. 13).

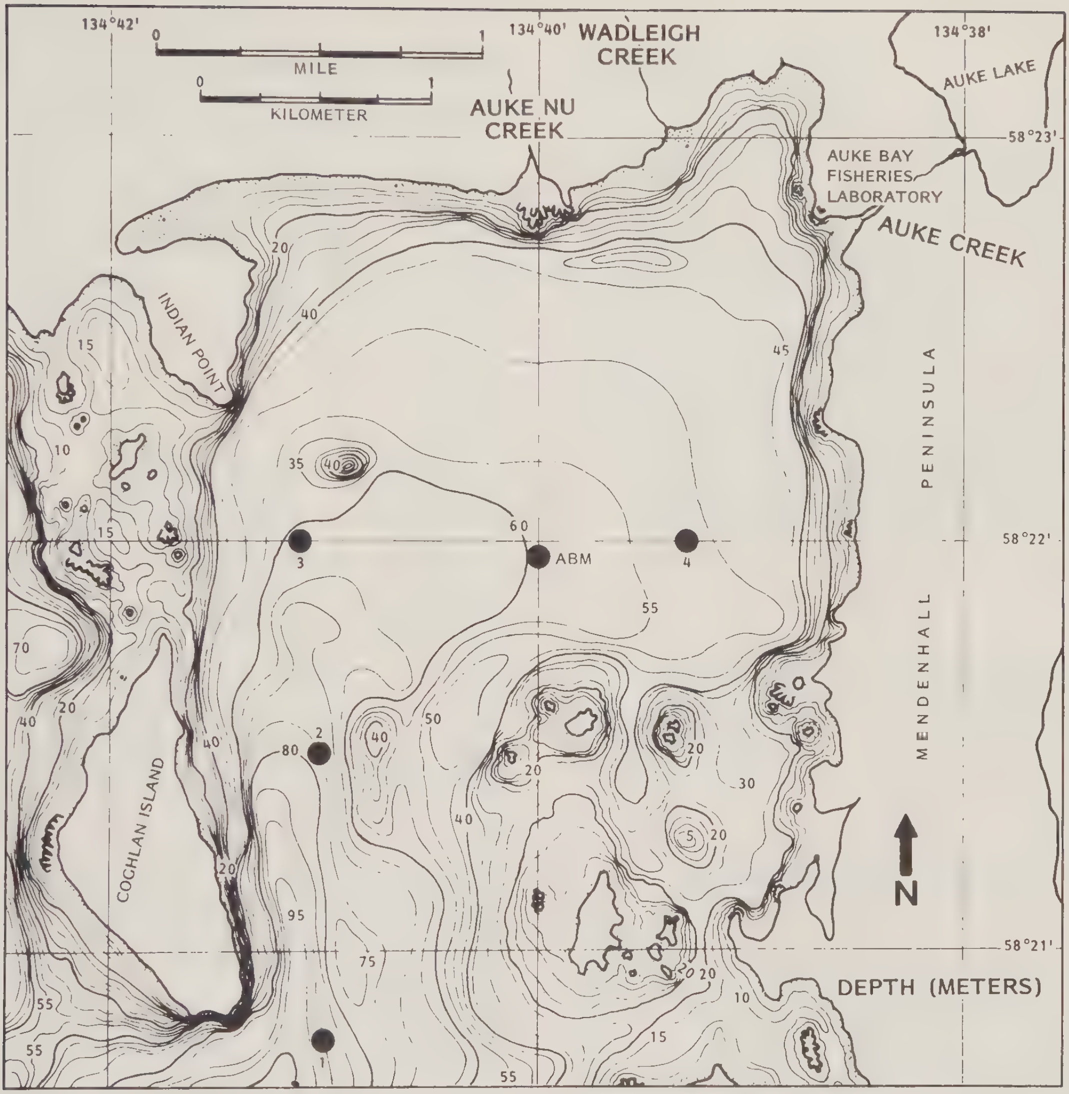
134°42'
0
1
MILE
0
1
KILOMETER
134°40'
WADLEIGH CREEK
AUKE NU CREEK
134°38'
AUKE LAKE
58°23'
AUKE BAY FISHERIES LABORATORY
AUKE CREEK
INDIAN POINT
PENINSULA
MENDENHALL
COGHLAN ISLAND
58°22'
58°21'
ABM
1
2
3
4
20
40
45
15
10
35
40
60
55
70
20
40
80
50
40
20
30
5
20
40
95
75
20
55
55
10
15
55
20
DEPTH (METERS)
N

Figure 2.—Bathymetry of Auke Bay, Alaska, and locations of oceanographic stations.

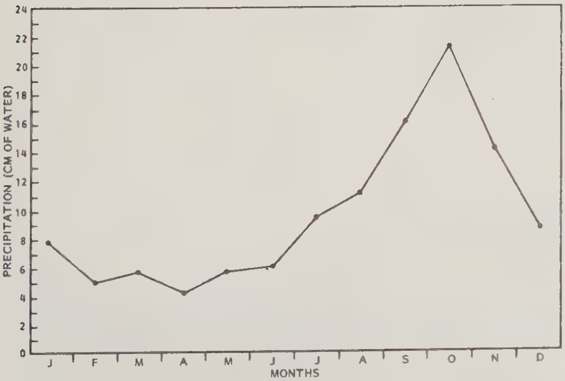

Figure 3.—Average monthly precipitation (cm of water) at Juneau airport, 1931-60. (See text footnote 2.)

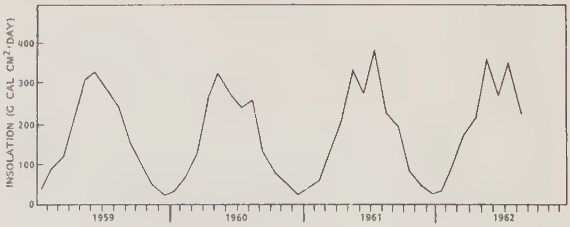

Figure 4.—Monthly averages of daily insolation (g-cal/cm^2/day) in Auke Bay area, 1959-62. (See text for calculation of insolation.)

Runoff

The streams entering directly into Auke Bay are small and drain low-elevation (less than 900 m) forested areas. The streams are fed by rainfall and melting winter snows, and discharge from them has several maxima and minima each year that vary in timing from year to year. These are Auke Creek, Auke Nu Creek, Wadleigh Creek, and several smaller unnamed streams.

The larger more distant Mendenhall River and Lemon Creek discharge into Fritz Cove and Gastineau Channel adjacent to Auke Bay. Their waters eventually enter Auke Bay. The watersheds of these larger streams are rocky slopes, ice and snow fields, and glaciers. The monthly discharge follows an annual cycle, with a single minimum in February or March and a single maximum in July (U.S. Geological Survey 1964). The winter minimum is caused by a decreased rate of snowmelt at higher elevation and the summer maximum by a combination of increased snowmelt and moderate precipitation.

Tides

The tides in Auke Bay are semidiurnal and show diurnal inequality. The mean tidal range is slightly more than 4 m (U.S. Coast and Geodetic Survey 1962). Spring tides exceed this by almost 2 m. The times and heights of high and low water are nearly the same over the entire Auke Bay area.

PHYSICAL AND CHEMICAL OCEANOGRAPHIC FEATURES OF AUKE BAY

The Northwest and Alaska Fisheries Center Auke Bay Laboratory has collected descriptive physical and chemical oceanographic data in Auke Bay since 1959. These oceanographic observations have been parts of a variety of projects with differing needs and goals, so the schedules and types of observations have varied over the years. The seasonal cycles described in this report are derived primarily from data collected from 1961 to 1967, supplemented by some earlier and later observations.

Five oceanographic stations (Fig. 2) were occupied monthly during 1961-63. The local variations within the bay were relatively small when compared with the frequent transient vagaries. Oceanographic properties appeared to be homogeneously distributed over the area of the bay, and differences were usually within the limits of error in our measurements. Consequently, beginning in March 1963, the five stations were replaced with a single midbay station, Auke Bay Monitor (ABM, Fig. 2) which was monitored monthly for 1 yr. From March 1964 through July 1967, the ABM station was occupied approximately weekly in order to define more precisely short-term variations in oceanographic conditions associated with use of amino acids as a nitrogen source by the phytoplankton (Bruce 1969).

The observations were made with conventional Nansen bottles and reversing thermometers from the research vessels *Sablefish* and *Murre II* and from various small boats. The accuracy of the temperature measurements was estimated ±0.05°C. Salinities during the years 1959-64 were measured by titration, accurate to ±0.01°/oo, and later by salinometer, accurate to ±0.05°/oo. Concentration of dissolved oxygen was measured by the conventional Winkler technique, accurate to ±0.1 ml/liter. Phosphates, nitrates, and silicates were determined by the methods of Strickland and Parsons (1960) and are believed within the precision limits of ±0.05, ±0.3, and ±3.0 μg-at./liter respectively.

Temperature

Water temperature is one of the most important characteristics of marine environments. The distribution of water temperature and salinity influences the physical mixing properties of the water. In addition, temperatures, along with salinities, are useful in identifying masses of water and in monitoring changes in physical and chemical properties of marine environments. Finally, temperature and temperature changes affect metabolism and other processes in marine plants and animals. Accordingly, this subject has been more fully investigated than any other physical factor.

The surface water temperature in Auke Bay ranged from less than 2° to 17°C; an extended minimum occurred between January and March and a maximum in August (Fig. 5). Sea surface temperatures were greater than the maximum air temperatures during the months of November to February, reflecting large heat losses to the atmosphere during the winter. Temperature variations were greatest at the surface and decreased with increasing depth (Fig. 6). At a depth of 50 m, the temperature ranged from 2° to 7.8°C. The month of maximum water temperature was progressively later in the summer at progressively greater depths. For example, the surface maximum was reached in August, and the maximum at 50 m was reached in October or November.

During the year vertical temperature profiles change from well mixed to strongly stratified (Fig. 7). In January

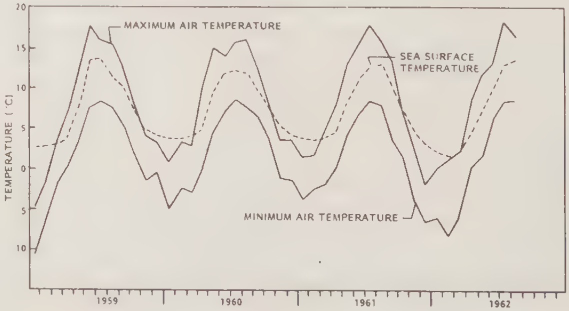

Figure 5.—Monthly averages of daily maximum and minimum air temperatures (°C) recorded at Juneau, Alaska, airport and of sea surface temperature (°C) at Auke Bay, Alaska, 1959-62.

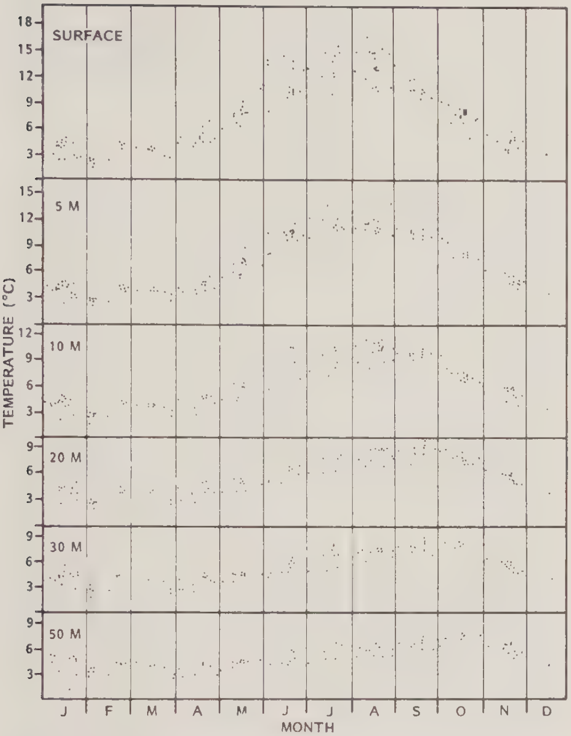

Figure 6.—Observed water temperatures (°C) at selected depths in Auke Bay, Alaska, 1960-68.

the water column is isothermal to a depth of 50 m. In April the surface waters begin to warm and start development of a thermocline. Between April and July, surface warming continues and by late July extends from 10 m. A lesser gradient in temperature exists from 10 to 30 m, and below 30 m the temperature changes very little. In the thermocline proper, a 10°C temperature difference may be encountered in July and August. After mid-September, the thermocline decays because of radiant heat losses and mixing by fall storms. The effect of storms is to change the distribution of heat, as illustrated by the decrease in the temperature of the surface waters to a depth of 10 m and a warming of the water below 10 m by vertical mixing. Between October and January, vertical mixing and cooling of the surface water continue, and in January conditions are again isothermal to a depth of 50 m.

Salinity

If we exclude those areas close to the outflow of large rivers or close to melting ice, the salinities of the world's oceans range from 32 to 38 °/₀₀. The salinities of estuaries, however, are much more variable in time and space, ranging from near zero to more than 30 °/₀₀. This wide variation is important as a selective agency in determining the composition and structure of biological communities.

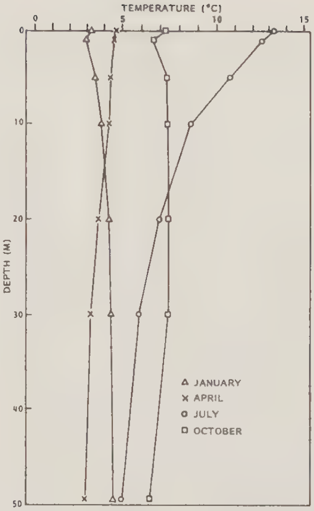

Figure 7.—Typical profiles of temperature (°C) in Auke Bay, Alaska, for January, April, July, and October; data are averages for 1960-68.

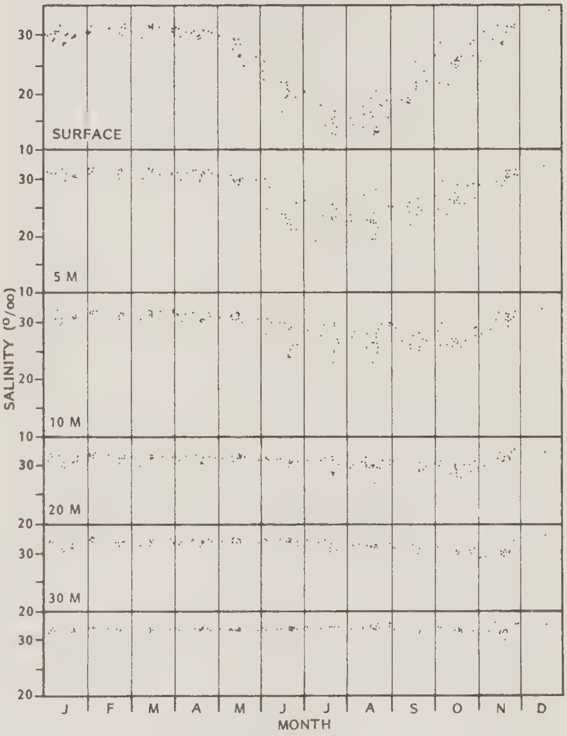

Figure 8.—Observed salinities (°/₀₀) at selected depths in Auke Bay, Alaska, 1960-68.

Variation of salinity at selected depths in Auke Bay from 1960 to 1968 is shown in Figure 8. In general, the annual cycle of salinity in the top 10 m was characterized by 1) a period from January to April when salinity remained between 29 and 31 °/₀₀, 2) a period between May and July-August when salinity decreased to a minimum of about 17 °/₀₀, and 3) a recovery period (September-December) when salinity increased again to the winter values. In deeper water (20 to 50 m) the salinity remained rather constant at 30 to 31°/oo through the year. The salinity of surface waters varied 3 to 5°/oo in a few days during the spring-fall period while short-term variations in the deeper water seldom exceeded 1°/oo.

Two distinct layers of water—surface (to 30 m) and deep (below 30 m)—appear in the vertical profiles of salinity in Auke Bay (Fig. 9). Between January and April, isohaline conditions exist from the surface to 50 m. The salinity of the surface layer decreases continuously from April through July or August, and a strong salinity gradient forms in the top 10 to 12 m. The strongest halocline occurs in July with salinities near 20°/oo at 5 m, 27°/oo at 10 m, and 31°/oo at 30 m. Surface salinity remains low through September and increases in October as a result of autumn storm mixing. The strong halocline of July and August is the result of peak runoff from the large, glacial-fed streams. Runoff from the low elevation, forested watersheds does not affect surface salinities as much as runoff from the glacial streams. Runoff from lower elevations peaks in both the spring and the fall, but not during the summer (McLain 1969). Often in the summer silty glacial Mendenhall River water intrudes from neighboring Fritz Cove into the clearer waters of Auke Bay.

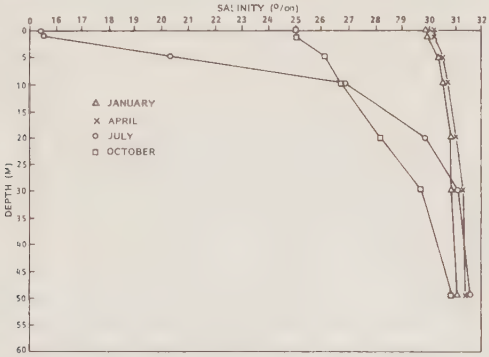

Figure 9.—Typical profiles of salinity (°/oo) in Auke Bay, Alaska, for January, April, July, and October; data are averages for 1960-68.

Density

Water density, a function of temperature and salinity, is used to identify water masses and to assess the stability or stratification and probable circulation of these water masses. Over the range of values observed in Auke Bay density is affected more by salinity variation than by temperature variation.

The annual cycle of water density of Auke Bay from 1960 to 1968 expressed in terms of σ_t[3] is shown in Figure 10. The density of the surface water in Auke Bay varied over a range of σ_t values between 9 and 24. Density was greatest and varied little with depth from December to April. In late April, density began to decrease at the surface and continued to decrease through July, reaching a minimum in August (mean minimum σ_t = 11.0). The change in σ_t occurred progressively later with increasing depths (Fig. 10). The minimum σ_t at 30 m was 22.2 in October. At 50 m the density was relatively constant and had no obvious maximum or minimum.

Figure 11 shows the seasonal vertical profiles of average σ_t. From January to April the water in Auke Bay is well mixed and the density is uniform from the surface to 50 m. From July to October there is a strong den-

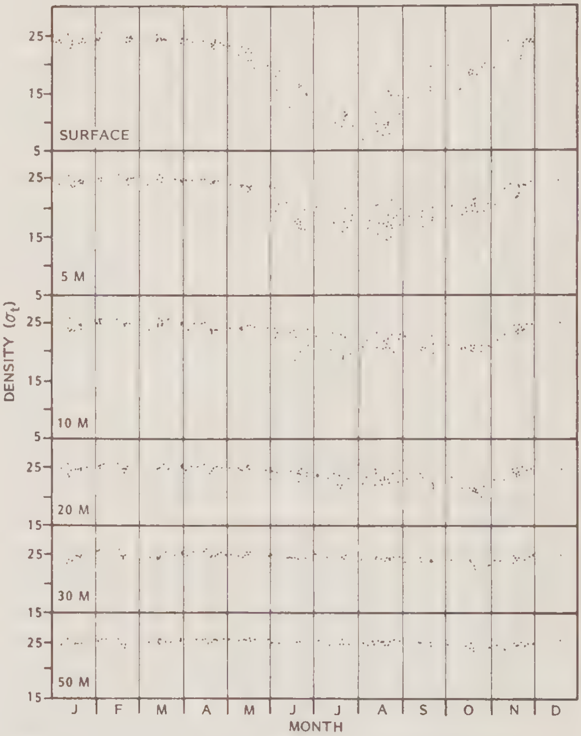

Figure 10.—Observed densities (as σ_t) at selected depths in Auke Bay, Alaska, 1960-68.

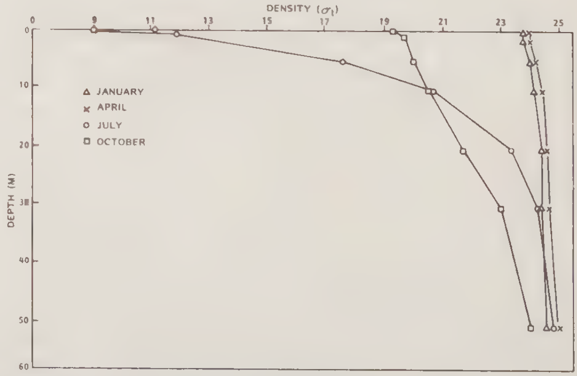

Figure 11.—Typical profiles of density (as σ_t) in Auke Bay, Alaska, for January, April, July, and October; data are averages for 1960-68.

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[3] Sigma-t (σ_t) = 1,000 (ρ-1) where ρ is the density of the water.

sity gradient from the surface down to 30 m. The data for all years of this study show the same seasonal pattern of density distribution.

Stability

Stability of a water column[4] is determined by the rate of change of density with depth, the vertical gradient of density. Where stability is high, vertical movement and vertical mixing are inhibited. The water column in a strong vertical gradient of density (a marked pycnocline) is very stable, and much more energy is required to displace particles of water upward or downward than in a region where the gradient is weak. This mechanism greatly restricts the vertical transfer of water from the deep layer to the upper layer in Auke Bay. Tidal-induced turbulence is unable to penetrate the pycnocline.

Table 1 gives numerical values for the stability of Auke Bay water during July and August 1965. All the stability values in Table 1 are positive and relatively high, indicating a highly stable water column. Data from other years show the same general density distribution as in 1965; all depict a highly stable water column during the summer. The similarity between seasonal cycles of salinity and density in Auke Bay (Figs. 8 and 10) is expected because of the strong dependency of density on salinity at the relatively low temperatures common in Auke Bay.

The development of a stable water column is one of the most ecologically significant features of the oceanography of Auke Bay because stability of the water column is a prerequisite for the onset of spring phytoplankton bloom (Riley 1942; Sverdrup 1953; Steele 1966). Gilmartin (1964) found that seasonal variability in the stability of the water column in a British Columbia fiord was the primary factor controlling phytoplankton growth. We observed a strong burst of phytoplankton growth each year in April or early May as solar radiation increased and a stable water column began to form. It is clear that stratification has a pronounced effect on the basic productivity of Auke Bay throughout the spring-summer growing season.

Dissolved Oxygen

Oxygen is one of the common gases dissolved in natural waters and is critically important because of its key role in biological energy transfers. Although aquatic organisms respire efficiently at oxygen concentrations considerably below saturation values, metabolic rates and efficiencies are dependent on the availability of dissolved oxygen. Consequently, the dissolved oxygen concentration is a major determinant of the environmental quality of water. The oxygen requirement of organisms is given generally in terms of absolute concentration expressed in appropriate units such as ml/liter or mg/liter.

Concentrations of dissolved oxygen at selected depths in Auke Bay are shown in Figure 12. Dissolved oxygen in the upper 5 m generally remained above 6 ml/liter, and spring and summer concentrations were above 8 ml/liter. Highest concentrations occurred from April through June and maximum observed value was 11.4 ml/liter. Below 10 m the concentration of dissolved oxygen decreased with depth. In winter the concentrations varied less with depths. The lowest concentrations of oxygen at or near the bottom occurred in September and October.

The degree of oxygen saturation provides information on the relative intensities of processes which affect the oxygen content of the water. Supersaturation is observed frequently and is essentially a result of high photosynthetic activity by plants in the upper layer of the water. Under conditions of high solar radiation during the day and abundant nutrients, the rate of oxygen production may exceed the rate at which oxygen is given

Table 1.—Stability (E)[1] at Auke Bay monitor station in July and August 1965.

	21 July 1965				10 August 1965			
Depth (m)	Temp. (°C)	Salinity (°/oo)	σ_t	10^6E	Temp. (°C)	Salinity (°/oo)	σ_t	10^6E
0	13.48	16.30	11.94		16.55	16.30	11.37	
				1,107				1,189
10	7.84	29.50	23.01		7.98	29.85	23.26	
				151				101
20	5.82	31.10	24.52		6.21	30.85	24.27	
				49				43
30	4.76	31.57	25.01		5.66	31.30	24.70	
				16				22
50	4.28	31.90	25.32		4.70	31.72	25.13	

[1] See text footnote 4.

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[4] For depths to 100 m, stability (E) can be expressed by

$$E = 10^{-3} \frac{d\sigma_t}{dZ} \text{ (Sverdrup et al. 1942, p. 417).}$$

or in different form

$$E = 10^{-3} \frac{(\sigma_{t_2} \quad \sigma_{t_1})}{(Z_2 \quad Z_1)}$$

where Z = depth
$dZ \cong Z_2 - Z_1$ = change in depth
$d\sigma_t \cong (\sigma_{t_2} - \sigma_{t_1})$ = change in σ_t
σ_t = $1{,}000(\rho - 1)$ where ρ = density of the water.

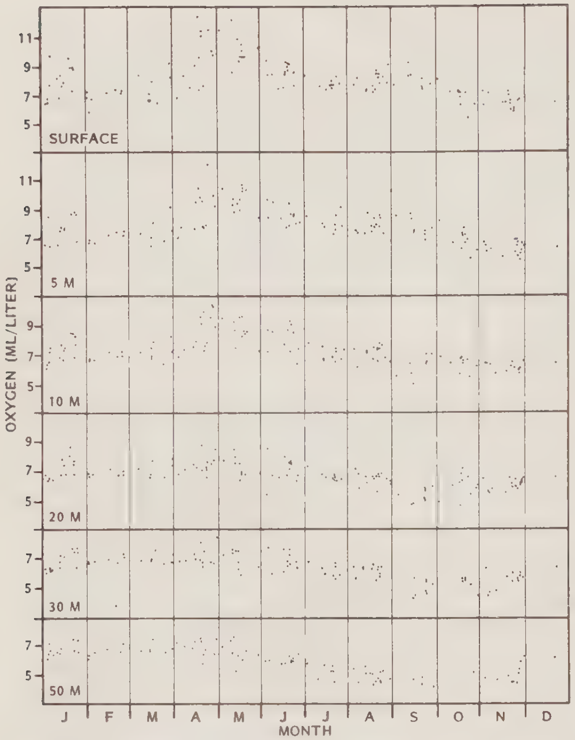

Figure 12.—Observed concentrations of dissolved oxygen (ml/liter) at selected depths in Auke Bay, Alaska, 1960-68; data are observed concentrations.

off at the surface, and supersaturation will occur. Appreciable supersaturation occurs in Auke Bay during the spring and summer, even down to 10 to 20 m (Fig. 13). This coincides with spring and summer phytoplankton blooms. Lowest concentrations of oxygen occur during the fall and winter when photosynthetic activity is reduced and bacterial decomposition and chemical oxidation of detritus lower the oxygen content.

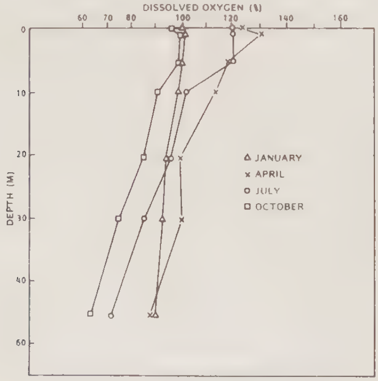

Figure 13.—Typical vertical profiles of percent saturation of dissolved oxygen in Auke Bay, Alaska, for January, April, July, and October; data are averages for 1960-68.

Inorganic Nutrients

The circulation of biologically active materials such as phosphate, silicate, and nitrate, as well as their distribution in the water column, depends on biological and physical processes and differs in detail from the circulation and distribution of water and its conservative properties. Because these materials are dissolved components of water, they are affected by advective and eddy diffusion processes. In addition, they are exchanged between the water and the biomass in a cyclic process. During periods of high biological activity, changes in the distribution and abundance of biologically active components of the water column may occur rapidly relative to changes due to physical processes alone. Thus, their study may add significantly to the physical description of an area.

During our study in Auke Bay, there was a regular seasonal cycle in concentrations of inorganic phosphate, silicate, and nitrate (Figs. 14, 15, 16). Maximum concentrations of all three nutrients occurred in winter (January-April), and all were uniformly distributed throughout the water column in this period. A rapid reduction of the three nutrients above 20 m in April was associated with the outburst of phytoplankton growth. In each year of our study, we noticed a marked rise in numbers of diatoms and chlorophyll concentrations and a corresponding drop in concentrations of phosphate, silicate, and nitrate (unpublished data on file Northwest and Alaska Fisheries Center Auke Bay Laboratory). Once stability is established in spring, high levels of photosynthetic activity rapidly deplete the available nutrients because vertical advection of nutrients into the surface is inhibited by the stability of the water column.

Raymont (1963) reviewed the distribution and amounts of phosphate, silicate, and nitrogen throughout the world oceans, including many of the important coastal and inshore areas. In comparison with other nutrient-rich coastal and inshore environments, the amounts of these materials in Auke Bay water were relatively high. Friday Harbor in western Washington had some of the highest observed concentrations of both phosphate and nitrate—about 1.8 μg-at./liter of phosphate and 21.0 μg-at./liter of nitrate (Raymont 1963). Riley and Conover (1956) found maximum phosphate and nitrate concentrations in Long Island Sound of 1.9 and 17.0 μg-at./liter, respectively. Maximum concentrations in Auke Bay were 3.5 μg-at./liter of phosphate and 26.0 μg-at./liter of nitrate. Maximum silicate concentrations in Auke Bay were also comparatively high—70.0 μg-at./liter. This is significantly greater than the maximum values reported for the English Channel, 5.0 μg-at./liter, or for Friday Harbor, 53 μg-at./liter (Raymont 1963). The highest silicate concentration reported anywhere was 160 μg-at./liter in the deep water of the North Pacific Ocean (Raymont 1963).

In general, throughout the summer, phosphate values in Auke Bay in the upper 5 m tended to remain low, although there were some fluctuations. Minimum concentrations of phosphate observed in surface water were

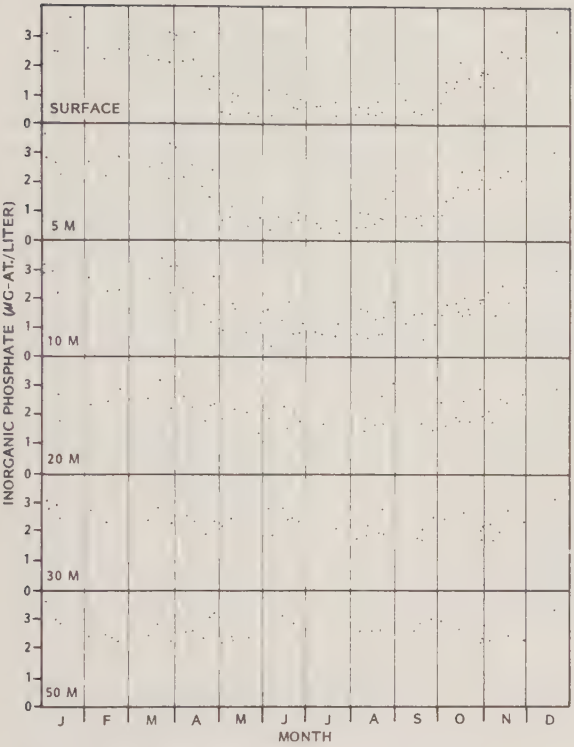

Figure 14.—Observed concentrations of inorganic phosphate (µg-at./liter) at selected depths in Auke Bay, Alaska, 1963-67.

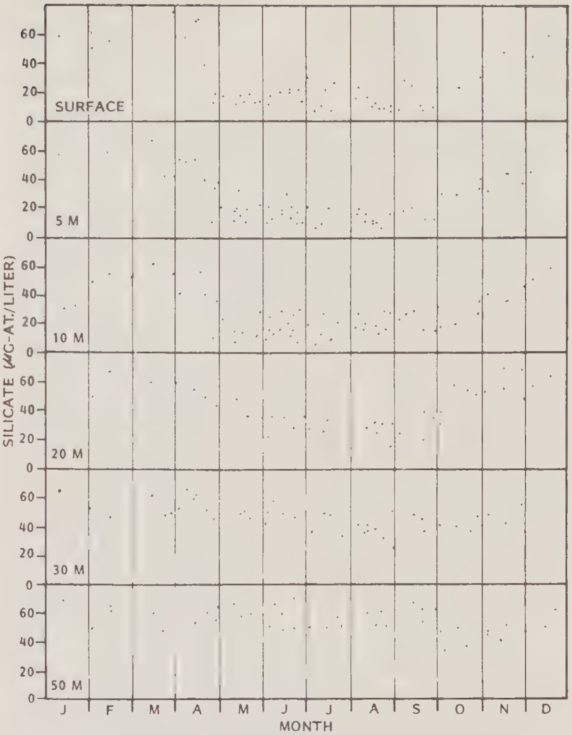

Figure 15.—Observed concentrations of dissolved silicate (µg-at./liter) at selected depths in Auke Bay, Alaska, 1963-67.

between 0.30 and 0.20 µg-at./liter, versus a winter high of 3.0 to 3.5 µg-at./liter (Fig. 14).

Short-term increases in phosphate concentrations in the top 5 m from May through August did not have a strong coincidence with periods of increased runoff. Hence, freshwater input was discounted as a significant cause of increases in nutrients, including phosphate, over short time periods (3 to 7 days). Studies by Curl, Iverson, and Conners[5] showed that tidal effects in Auke Bay were not sufficient to mix nutrient-rich water into the euphotic zone, but that wind-induced mixing through the pycnocline could be caused by winds of 4 m/s persisting for 24 h or longer.

Although the causes of fluctuation in phosphate levels are not clear, the most probable causes are regeneration of inorganic phosphate from organically bound phosphate and wind-induced vertical mixing of inorganic phosphate through the pycnocline. Laboratory measurements of the rate of phosphate regeneration (Cooper 1935) indicate that up to one-half of the total phosphorous content of decomposing plankton appears in soluble form within 24 h.

The silicate cycle in Auke Bay (Fig. 15) generally paralleled the phosphate cycle; this similarity was also demonstrated by Richards (1958) in the western Atlantic. Studies in the English Channel by Atkins (1930) showed that silicate was depleted and regenerated simultaneously with phosphate.

While phosphate and silicate in Auke Bay had the same general seasonal patterns of distribution, some differences appear when the data are examined in detail: short-term variation in concentration of phosphate occurred primarily in the upper 5 m of the water column (Fig. 14); the greatest variations in silicate occurred between 10 and 20 m (Fig. 15). Variability in the concentration of silicate throughout the water column in Auke Bay is generally greater than it is for phosphate.

Minimum silicate concentrations of 2 to 4 µg-at./liter occurred in the surface water of Auke Bay during July, August, and September (Fig. 15). Short-term increases occurred in late June and early July, when the proportion of dinoflagellates (phytoplankton which do not utilize silicate) to diatoms was quite high. We interpreted this increase as a reflection of the difference in rate of uptake by the relatively small number of diatoms present and the rate of in situ regeneration, plus advective input.

Maximum silicate concentration of about 60 µg-at./liter occurred throughout the water column from December through the middle of March—a high concentration even for inshore waters. Offshore waters usually contain an order of magnitude less silica, although the level is quite variable.

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[5] Curl, H. C., Jr., R. L. Iverson, and H. B. O'Conners, Jr. 1971. Pelagic ecology of biological production in Auke Bay, Alaska. Final report to National Marine Fisheries Service, Auke Bay Fisheries Laboratory, Auke Bay, Alaska, Contract 14-17-0005-207.

The nitrate cycle in Auke Bay paralleled in general the phosphate and silicate cycles. Maximum concentrations of 24 to 28 μg-at./liter were present throughout the water column during the winter period (Fig. 16). The reduction of nitrate in the top 5 m from 24-28 μg-at./liter to 0.5 μg-at./liter with the outburst of phytoplankton growth in April is more drastic than in phosphate and silicate.

The short-term fluctuations that occurred in concentrations of phosphate and silicate did not occur in nitrate concentrations. The top 5 m were essentially depleted of nitrate by May and remained impoverished through August. We attribute this to a slow regeneration rate of nitrate from organic combinations, which according to the experiments by Brand and Rakestraw (1941) requires 3 or 4 mo. Riley (1967) presented indirect evidence that the nitrogen cycle is significantly slower than the phosphate cycle.

The summer pycnocline is enough of a barrier to prevent nitrate from reaching the surface in any significant quantity (this is true also for phosphate and silicate), except during periods when wind velocity is at least 4 m/s for at least 24 h. Periodic measurements of the nitrate content of fresh water entering Auke Bay show that only negligible amounts of nitrate enter the bay from these sources.[6]

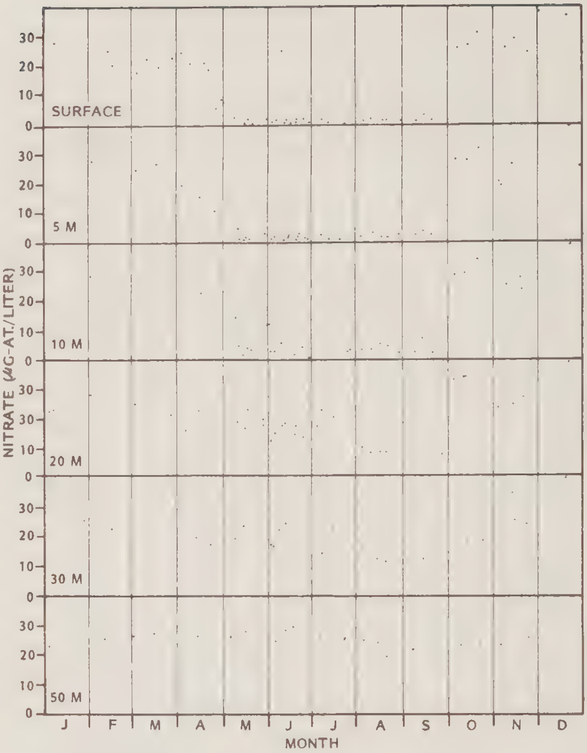

Figure 16.—Observed concentrations of dissolved nitrate (μg-at./liter) at selected depths in Auke Bay, Alaska, 1963-67.

SUMMARY

This study has described temporal variation in oceanographic conditions over an 8-yr period and provides background information on environmental variability for future detailed studies of the ecology of Auke Bay. Salient environmental features of an annual cycle in Auke Bay are summarized below.

Auke Bay is about 130 km from the open ocean and is relatively isolated from direct oceanic moderation and from major circulation patterns of the main passages and straits in southeastern Alaska. The bay is strongly influenced by land runoff and by the local climate. The annual oceanographic cycles closely follow local atmospheric cycles.

By the end of the second week in April, the water column began to stratify because of increased absorption of solar radiation in the upper 5 m and the accumulation of fresh water on the surface from increased runoff and precipitation. As the spring-summer season progressed, stratification increased until a strongly developed pycnocline essentially isolated the upper 12 to 20 m from the deeper water.

Full development of the brackish surface layer in Auke Bay occurred in late July or August. In September, cooling of surface water coupled with wind mixing due to fall storms broke the density stratification developed during the spring-summer period. Nutrient-rich water below the pycnocline was mixed into the euphotic zone to replenish the nutrient-impoverished surface water, and a fall phytoplankton bloom occurred.

As the season progressed into fall, decreasing temperatures and increasing salinities in the surface layer of water increased the density of the surface water, resulting in thermohaline circulation which thoroughly mixed the water column. Hence, during the winter, the water column was essentially homogeneous, and the concentrations of phosphate, silicate, and nitrate throughout the water column were high. A well-mixed water column and low solar radiation prevented any significant phytoplankton growth during the winter; consequently, the distribution of biologically active dissolved components depended almost totally on physical processes during the winter.

The seasonal pattern described was repeated each year during the 8-yr period that routine observations were made.

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[6] Unpublished data on file Northwest and Alaska Fisheries Center Auke Bay Laboratory, NMFS, NOAA, P.O. Box 155, Auke Bay, AK 99821.

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To The Editor of Biometrics:

On Jensen's Comparison of Logistic Equations for Population Growth

In a recent issue of this Journal, Jensen (1975) compared different logistic equations of population growth and applied a production model to data on brook trout. He arrived at several conclusions, which we believe are unwarranted and caused by errors of several types. These errors are discussed here in the order in which they occurred in Jensen's paper.

First, Jensen inappropriately used a derivation of equation (1), $\frac{dN}{dt} = rN\left(\frac{K-N}{K}\right)$, (Pielou 1969) to arrive at the conclusion that equation (2), $\frac{dN}{dt} = bN\left(\frac{K-N}{K}\right)$, is more realistic than equation (1) as it describes the birth and death processes more realistically. He did this by using and extending Pielou's derivation to show that the limit of the birth rate, $\lambda(N) = a_1 - b_1N$, and the death rate, $\mu(N) = a_2 + b_2N$, as the population reaches equilibrium is 0. This result was obtained because Jensen misinterpreted Pielou's analysis. Pielou stated in her proof that as "the population reaches equilibrium at the saturation level, the birth rate and the death rate are equal" (page 22). This statement does not exclude the possibility that both the birth and death rates are zero; however, Pielou omitted this condition by defining a_1, $a_2 > 0$ and b_1, $b_2 \geq 0$ for $\lambda(N)$ and $\mu(N)$. Therefore, since the death rate is always greater than zero, the birth and death rates could never be zero and equation (1) still gives a realistic biological outcome.

Second, Jensen was apparently unaware of Pielou's definition of $\lambda(N)$ and $\mu(N)$ as linear functions as he defined $\lambda(N)$ and $\mu(N)$ as nonlinear functions and showed that the growth equation will never be logistic. He stated that there are three cases in which an equilibrium between births and deaths can be approached: A) a constant instantaneous birth rate per individual and an instantaneous death rate per individual which approaches the birth rate as the carrying capacity is approached, B) a constant instantaneous death rate per individual and an instantaneous birth rate per individual which approaches the death rate as the carrying capacity is approached, and C) an instantaneous birth and death rate per individual which approaches a constant value as the carrying capacity is reached (Wrigley 1969). Jensen, by defining $\lambda(N)$ and $\mu(N)$ as linear functions, showed that Case A gives the logistic equation. Then by choosing two non-linear functions for $\lambda(N)$ and $\mu(N)$ in Cases B and C, he concluded that only in Case A will the growth equation of a population be logistic. This conclusion is not true. Pielou's derivation gives all three of these cases in her generalized equations for $\lambda(N)$ and $\mu(N)$ and, as long as $\lambda(N)$ and $\mu(N)$ are linear, the growth equation will always be logistic.

Finally, Jensen's application of the production model to data on brook trout (McFadden, Alexander and Shetter 1967) contained a number of errors. The data of McFadden *et al.* started with the 1949 cohort, which Jensen used and labeled erroneously as the 1947 cohort. He also stated that the instantaneous fishing mortality rate was estimated as $F = 0.35$ by McFadden *et al.* Actually McFadden *et al.* estimated an annual fishing mortality rate of 0.35 which is not the same as an instantaneous rate. Furthermore, Jensen used a group of equations utilizing data from the life table of an exploited population to estimate r, the intrinsic rate of population increase, which he then equated to the parameter k in the logistic surplus production model. His estimate of r was incorrect since it should have been derived from data generated by an unexploited population. As a result his estimate of the intrinsic rate of population increase was negative and his results from the production model analysis were unreasonable.

We have shown that errors in interpreting and extracting data from published sources as well as misinterpretations of analytical results led Jensen to unwarranted conclusions. We hope this letter accompanied by Jensen's response will provide a clearer understanding of the logistic growth equation.

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Pielou, E. C. (1969). *An Introduction to Mathematical Ecology*. Wiley-Interscience, New York.

Wrigley, E. A. (1969). *Population and History*. McGraw-Hill, New York.

The author replied as follows:

I assumed that because $\lambda(N) = b - bN/K$ and $\mu(N) = d - dN/K$ gave $dN/dt = rN - dN^2/K$, that these were the birth and death rates per individual for equation (1). As stated by Coan and Francis this is not a valid argument because other expressions for $\lambda(N)$ and $\mu(N)$ also lead to the equation $dN/dt = rN - rN^2/K$. As a result, I do not succeed in showing that the birth rate and death rate in equation (1) approach zero as the carrying capacity is approached.

I still think the meaning of equation (1) is unclear. To derive equation (1) from equation (6) it must be assumed that $a_1 - a_2 = r$. My analysis shows that $a_1 - a_2$ is not the instantaneous rate of increase per individual as this would mean that the maximum sustainable yield of every fish population is zero. It often is assumed that $a_1 - a_2$ is the maximum instantaneous rate of increase per individual but in the logistic equation the instantaneous rate of increase per individual, $\frac{1}{N}\frac{dN}{dt}$, has no maximum for $N > 0$. At best it can be said that $a_1 - a_2$ can be approximated by determination of r in an "uncrowded condition." The parameter $a_1 - a_2$ relates the instantaneous rate of change per individual, which is a function of population size, to the degree of saturation.

I did not realize that cases *A*, *B* and *C* could be described by equation (6). As a result of the equations I used for $\lambda(N)$ and $\mu(N)$ I incorrectly concluded logistic growth occurred only in case *A*. If equation (6) is applied, the growth equations for all three cases are logistic but all are of somewhat different form. Only the parameters of the equation $dN/dt = bN - bN^2/K$, which is obtained in case *A* if $a_2 = 0$, can be estimated directly from a life table. This appears to be the only case in which the parameters a_1, a_2, b_1 and b_2 can be identified directly in terms of r, b and d.

McFadden, Alexander and Shetter (1967) estimated the annual fishing mortality of ages 0–I as 23.6 percent and the annual fishing mortality of ages I–II as 35.1 percent. Fishing mortality for other age groups could not be determined but most fish caught by anglers were aged 0–II. I took the simple mean of 23.6 and 35.1 to obtain an annual mortality of 29.3 percent which gives an instantaneous mortality coefficient of about 0.35 as stated in my paper. If I use 35 percent as the annual mortality I obtain an instantaneous fishing mor'ality coefficient of 0.43 which is even closer to the optimum value of 0.47 calculated from the surplus production model based on the equation $dN/dt = bN - bN^2/K$.

The life table I used is the 1949 life table as stated by Coan and Francis and not the 1947 life table as I stated in my paper.

Exploitation is irrelevant as concerns estimation of r from a life table. Lotka showed that if the birth rate per individual and the death rate per individual are constant, the population growth equation converges to the equation $dN/dt = rN$ and he provided an equation for calculation of r. No statement is made concerning the sources of mortality (Keyfitz 1968). For the brook trout population the mortality and fecundity appear to have been constant for many years and the parameters of the equation $dN/dt = bN - bN^2/K$ can be calculated from a life table.

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MFR PAPER 1251

Modified Tuna Purse Seine Net Achieves Record Low Porpoise Kill Rate

JAMES M. COE and PHILIPPE J. VERGNE

Earlier this year the Southwest Fisheries Center (SWFC) of the National Marine Fisheries Service (NMFS), La Jolla, Calif., released a gear research cruise report which described results of one of the latest efforts in the NMFS program to develop gear and techniques designed to reduce porpoise mortality in commercial tuna purse seining operations. The following information, taken from this cruise report, was prepared by James M. Coe, Fishery Biologist, SWFC, and Philippe Vergne of the Porpoise Rescue Foundation.

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The cruise described in this report extended from 7 October 1976 to 9 December 1976. The area involved was the yellowfin tuna fishing grounds off Mexico and Central America within the Inter-American Tropical Tuna Commission's yellowfin regulatory area.

VESSEL AND EQUIPMENT

The tuna purse seiner MV *Elizabeth C. J.* was chartered for this cruise, with Nicholas L. Lavalouis as master, Manuel Jorge, fish captain, and Joe Jorge, alternate fish captain. The vessel, 252 feet long with a 42-foot beam and a draft of 21 feet, can carry up to 1,700 tons of frozen tuna in 10 pairs of brine wells. Propulsion is provided by a twin-screw system with two 2,800-horsepower main engines giving a top cruising speed of 18 knots; a 400-horsepower bow thruster aids in maneuverability. The net used during the cruise was 700 fathoms long by 13 standard 4¼-inch mesh strips deep. The experimental "super apron" and double-depth safety panel of 1¼-inch mesh webbing (Fig. 1) were installed in the backdown area of the net.

PURPOSE AND OBJECTIVES

Purpose of the cruise was to test a modification of the "Bold Contender" system, termed the "super apron," and to develop techniques for its efficient use in reducing incidental porpoise mortality during commercial tuna purse seining operations. This work was done in partial conjunction with tuna-porpoise behavioral studies made during a portion of the same cruise period.

In addition to evaluating the effectiveness of the "super apron" modification of the "Bold Contender" system in reducing incidental porpoise mortality, other objectives of the cruise were: 1) to adjust flotation and deployment techniques during backdown to reduce the incidence of a prematurely submerged corkline and the resultant accidental loss of fish; 2) to adjust flotation and apron structure to permit controlled sinking of the backdown apex; and 3) to conduct further tests of the use of a small, one-man inflatable raft to assist in porpoise removal during and after backdown.

RESULTS

During the cruise, 30,233 porpoise were captured and 915.5 tons of yellowfin tuna were taken in 45 net sets on

Figure 1.--"Super apron" modification of the "Bold Contender" system, 16 December 1976, assembly diagram (vertical distances not to scale)

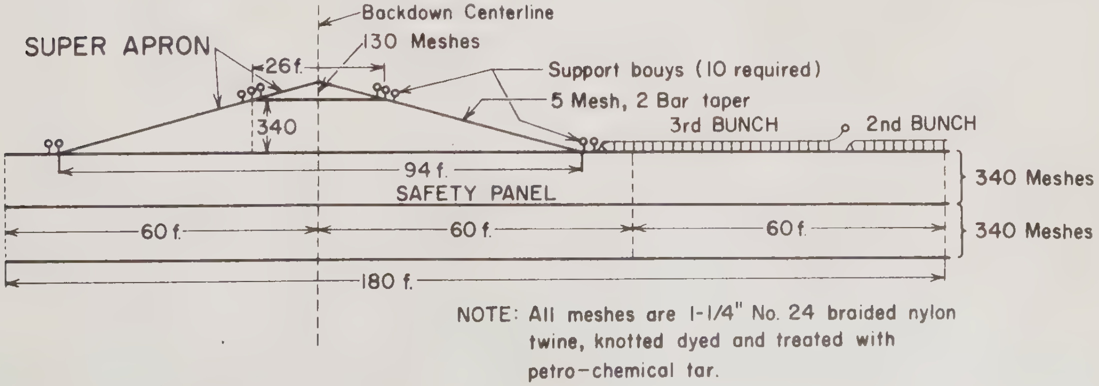

Table 1.—Data summary.

No. sets	Reason segregated	Tons tuna	Porpoise caught	Porpoise mortality	Kill per ton	Kill per set	Captured porpoise (percent) killed
15	Behavioral experiment	361.0	8,592	12	0.03	0.80	0.13
26	Gear-experimental sets without gear malfunction	492.5	19,512	4	0.008	0.15	0.02
5	Gear-experimental sets with gear malfunction	62.0	2,129	0	0	0	0
2	Schoolfish sets	95.0	—	—	—	—	—
48		1,010.5	30,233				

[1]Includes 5 tons skipjack tuna

Table 2.—Set data.

Set no.	Exp. set no.	Date	Lat (N)	Long (W)	Average crew est. of porp caught	% spin in porp caught	Tons[1] YF	Speed-boats used to tow	Elapsed back-down time (min)	# Raft rescued during back-down	# Porp live in net after back-down	# Raft rescued after back-down	Spotter killed	East spinner killed	White-belly spinner killed	Other killed	Total killed
1		10-14	18°32′	113°55′	533	—	45	0	20	3	0	0	0	0	0	0	0
2		10-14	18°27′	113°52′	325	—	35	1	8	2	0	0	0	0	0	0	0
3	1	10-16	11°19′	113°02′	water set	—	0										
4	2	10-17	10°33′	109°25′	1,350	13	65	0	16	5	1	1	6	1	0	0	7
5	3	10-18	11°15′	109°25′	950	3	25	0	20	0	0	0	1	0	0	0	1
6		10-19	10°45′	109°00′	275	—	12	0	20	0	0	0	0	0	0	0	0
7	9	10-20	10°25′	108°38′	350	1	~~15~~	0	9	1	0	0	0	0	0	0	0
8		10-20	10°22′	108°49′	975	30	25	0	13	0	0	0	0	0	0	0	0
9		10-23	10°52′	107°42′	175	—	5	0	14	0	0	0	0	0	0	0	0
10	6	10-25	9°33′	104°46′	213	—	10	0	25	0	0	0	0	0	0	0	0
11	7	10-26	9°14′	105°16′	1,066	10	70	0	19	8	0	0	0	0	0	0	0
12	8	10-27	9°21′	105°38′	183	—	18	2	9	3	0	0	4	0	0	0	4
13	4	10-27	9°46′	105°47′	1,033	17	65	2	10	5	0	0	0	0	0	0	0
14	5	10-28	9°45′	105°03′	300	—	8	0	11	3	0	0	0	0	0	0	0
15	10	10-29	9°44′	104°37′	1,000	12	55	0	11	2	0	0	0	0	0	0	0
16		10-30	9°41′	104°40′	125	—	15	0	11	3	0	0	0	0	0	0	0
17	11	10-31	9°37′	107°22′	90	—	4	2	10	4	1	1	0	0	0	0	0
18	12	10-31	9°46′	107°54′	625	45	6	2	8	3	0	0	0	0	0	0	0
19	13	11-1	10°36′	107°52′	816	1	8	1	8	0	0	0	0	0	0	0	0
20		11-1	10°43′	109°06′	1,066	6	30	1	17	0	0	0	0	0	0	0	0
21	14	11-2	10°40′	109°27′	283	—	8	1	9	4	0	0	0	0	0	0	0
22		11-2	11°27′	109°50′	766	—	8	0	26	2	4	3	0	0	0	1	1
23		11-4	18°21′	113°23′	866	78	10	1	16	5	0	0	0	0	0	0	0
24		11-4	18°34′	113°54′	933	5	50	0	7	5	0	0	0	0	0	0	0
25		11-5	18°40′	113°30′	1,033	13	20	1	15	7	0	0	0	0	0	0	0
26		11-5	18°23′	113°30′	683	15	5	1	20	0	0	0	0	0	0	0	0
27		11-9	13°53′	104°21′	683	—	10	0	11	6	0	0	0	0	0	0	0
28		11-11	13°58′	101°35′	833	—	12	0	15	10	0	0	0	0	0	0	0
29		11-11	14°14′	101°34′	683	0	9	1	13	5	0	0	0	0	0	0	0
30	15	11-12	13°43′	101°39′	333	0	4	0	15	3	0	0	0	0	0	0	0
31		11-12	13°34′	101°28′	55	0	0	0	6	1	0	0	0	0	0	0	0
32		11-13	12°20′	102°51′	700	0	4	0	12	5	0	0	0	0	0	0	
33		11-15	9°15′	100°18′	Sch. F	—	0										
34		11-16	9°20′	98°20′	266	—	45	1	10	4	0	0	0	0	0	0	0
35		11-16	9°08′	98°03′	433	—	12	1	8	2	0	0	0	0	0	0	0
36		11-18	10°15′	98°09′	Sch. F	—	90										
37		11-19	10°01′	97°31′	86	—	25	1	8	1	0	0	0	0	0	0	0
38		11-19	9°36′	97°15′	316	—	14	0	10	3	0	0	0	0	0	0	0
39		11-20	9°18′	97°50′	106	—	10	0	6	2	0	0	0	0	0	0	0
40		11-21	9°27′	97°46′	1,400	—	35	1	12	3	0	0	0	0	0	0	0
41		11-21	9°42′	97°44′	266	—	16	1	13	0	0	0	0	0	0	0	0
42		11-21	9°45′	97°54′	300	—	7	1	12	2	0	0	0	0	0	0	0
43		11-23	15°30′	101°27′	1,233	65	12	0	16	15	0	0	1	2	0	0	3
44		11-26	19°38′	111°21′	800	—	15	0	17	5	0	0	0	0	0	0	0
45		11-27	18°21′	114°18′	233	5	10	0	24	7	0	0	0	0	0	0	0
46		12-2	10°52′	109°53′	2,500	5	32	0	12	3	0	0	0	0	0	0	0
47		12-5	19°13′	111°49′	550	—	25	0	15	4	0	0	0	0	0	0	0
48		12-6	18°55′	112°50′	1,666	95	1.5	0	15	0	0	0	0	0	0	0	0
Total (behavior sets)					8,592		361	10	180 (Avg 12.86)	41	2	2	11	1	0	0	12
Total (gear sets)					20,864		644.5	12	422 (Avg 13.61)	105	4	3	1	2	0	1	4
Total (all sets)					29,456		1,005.5	22	602 (Avg 13.38)	146	6	5	12	3	0	1	16

[1]Tonnages are estimates made at time of set, not actual unloading weights

yellowfin tuna associated with porpoise. One set was a water set and two sets were made on tuna associated with floating objects (logs) in which 90 tons of yellowfin and 5 tons of skipjack tuna were landed. Table 1 presents a summary of the catch and kill data for the behavioral research and gear research sets. Table 2 presents the date, location, catch, kill, and raft-use statistics by set with subtotals for the gear and behavioral sets.

Porpoise mortality occurred on only 5 of 45 sets made on tuna-porpoise-associated schools. Sixteen porpoises were killed on these 5 sets—4 during the course of regular fishing operations and 12 during the activities of the scientific party. Excluding mortality during scientific activity, the mortality rates were 0.09 per set, 0.004 per ton of yellowfin caught in association with porpoise, and 0.013 percent of the porpoise captured.

Fourteen net sets were made for the purpose of studying porpoise behavior in detail. As many as three skiffs and six divers were inside the net prior to and during backdown. In three of these sets (numbers 4, 5, and 12) the presence of the divers and tagging efforts during backdown hampered porpoise release and resulted in 12 of the 16 deaths. The remaining four deaths occurred during backdown in two gear experimental sets that had no operational malfunctions. The animals became folded into the side of the backdown channel at a depth that precluded hand rescue.

The extremely low porpoise mortality rate experienced during this cruise was the result of the care and efficiency of the fishing captain and crew members in setting and hauling their net, using speedboats to adjust the corkline (18 sets), and in backing down until all live porpoise were released (42 of 45 sets). These efforts, in conjunction with the "super apron" and double-depth safety panel of 1¼-inch stretch-mesh webbing, allowed this vessel to achieve a record low kill rate.

The "Super Apron"

The apron-type appendage to the backdown area of purse seine nets was first tried on an NMFS-chartered vessel in the fall of 1974 and subsequently led to the development and successful testing of the apron-chute complex known as the "Bold Contender" system, 1 year later. It includes a porpoise safety panel of 1¼-inch mesh webbing 12 fathoms deep and 180 fathoms long. A 10-vessel mass test of the "Bold Contender" system in 1976 resulted in mortality rates substantially below the 1976 fleet averages for vessels using conventional nets, i.e., 2-inch stretch mesh in the safety panel. However, the mass testing revealed two generally recognized problems with its use. First, the smaller mesh size of the safety panel and apron-chute complex caused considerably greater drag when being pulled through the water during backdown than did the normal 2-inch safety panel. This caused the corkline perimeter of the backdown channel to submerge in the early stages of backdown, thus increasing the danger of loss of fish and necessitating a slower-than-normal backdown. Secondly, several vessels reported that the inability to sink the corkline at the apex of the backdown channel in the later stages of the procedure caused greatly increased need for hand rescue and longer backdown times.

To alleviate these problems, the two-stage taper employed in the "Bold Contender" system (five mesh, two bar on the apron and one mesh, two bar on the chute) was changed to all five mesh, two bar. This straight taper allowed more even distribution of the downward pull on the corkline as backdown proceeded. Although the corklines did tend to sink slightly in the early stages of backdown, and backdown still had to begin slowly, no fish were lost at this stage during the charter and it was generally agreed that there was no problem.

With the "super apron" modification, the topmost strip of 1¼-inch webbing (designated as the chute in the "Bold Contender" system) is approximately 200 meshes shallower at the backdown apex than its predecessor. The fish captain was able to sink the backdown apex to release the porpoise at will during all stages of the procedure. The resurfacing of the corkline after sinking was probably slightly slower than for nets with the 2-inch porpoise safety panel. Two or three speedboats were deployed at the backdown channel apex on every set to help prevent accidental fish loss and to hand-release porpoise as needed. The chief scientist estimated that approximately 18 tons of tuna were accidentally backed out of the net during porpoise release in the 45 porpoise sets during the cruise. In general, the fish captain and the alternate fish captain were pleased with the porpoise-saving characteristics of the "super apron."

Observations from the inflatable raft during backdown on the charter of the MV *Bold Contender* (fall 1975) showed that spotted porpoise sometimes became passive and piled up on the bottom of the backdown channel where they could be mistaken for dead. The removal of the extra webbing in the chute (discussed above) eliminated the two-step shelf formed with the "Bold Contender" system. Thus, as backdown proceeded with the "super apron," the channel became progressively shallower and ramp-like, raising the "passive" spotters up and flushing them out of the net. This reduced the necessity for hand rescue considerably. Of the 146 animals hand-released from the raft during backdown, the rescuer was quite certain that most of them would have been backed out anyway. No porpoise were killed in the six porpoise sets for which the raft was not used.

The use of the "super apron" atop the small-mesh, double-depth safety panel is not without operational faults, primarily because of the increased drag of the small mesh as it is moved through the water or as it is held against a current. In each of the porpoise sets which caught 50 tons of tuna or more the corkline tended to sink after backdown in the area just outboard of the third bow bunch. Though only a few tons of tuna were lost in porpoise sets, approximately 35 tons were lost in set 36 (schoolfish on a log) in this area. Underwater observation of the net in that area showed that as the net is hauled in after backdown the small mesh squeezes the entrapped water against the bunches which act as a dam. The blocked water forces the small mesh outboard of the third bow bunch to canopy out and when stretched to its limit the corkline begins to sink. The faster the net was rolled the more rapidly water had to be squeezed out and the deeper the corkline sank. It was found that this kind of sinking could be alleviated easily by release of the third and second bunches slightly earlier than normal. With large catches (>50 tons) it may be necessary to roll the net aboard a little more slowly.

On set 33 (schoolfish with a log) a very strong surface current and an oblique subsurface current caused the entire area of small mesh from the second bow bunch to mid-net to sink and stay down until the purse rings were brought up out of the deep current. The surface current moved the log and almost all of the fish over the sunken corkline. It was not possible to judge the degree to which the small mesh was responsible for the sinking but it surely contributed to it. To avoid this problem in areas of strong currents, the captain must note the current direction and position all sets to avoid pursing the small mesh area of his net against the current.

As with the "Bold Contender" system, there is a tendency for the center of the "super apron" to fold into or out of the net in some sets. On 15 sets a speedboat was used without incident to open or adjust the backdown apex prior to backdown. No maintenance was required on the small mesh during the cruise and only a few broken meshes and shark holes were seen by the underwater observer.

Inflatable Raft

During 39 of 45 porpoise sets, a small inflatable raft was used as an observation-and-rescue platform by one of the scientists employing a mask and snorkel. The raftman signaled the captain when the backdown release area was clear of fish. In addition, he assisted in the removal of the last few porpoise in the late stages of backdown. Generally, backdown was continued until the raftman signaled that all porpoise including the "passive" spotters had been released.

In checking to see if all live porpoise were out of the net, it was discovered that the raftman could hear vocalizations of porpoise that were still in the net but could not be seen. This final listening check became common practice and several animals were saved as a result.

The raft was also used during backdown to herd the porpoise toward the release area. This seemed to work well but only if the raft stayed more than about 10 meters from the nearest animals. When some groups of porpoise (10 to 100) would refuse to go over the corkline during backdown the raftman would wait until they were congregated near the sunken corkline and then paddle straight at them making as much commotion as possible. The initial avoidance response of the nearest animals often started them over the corkline and backdown would proceed to completion.

In four sets with expected large catches of fish the raft was used to attach up to four flotation balloons to the corkline along the sides of the backdown apex to lessen the chance of fish loss if all of the fish happened to move into the apex at one time. This was probably a good safeguard but it was never really tested with a large catch. After backdown the balloons were collected in the raft to facilitate net retrieval.

SUMMARY

The record low mortality rate experienced on the charter cruise is the result of the concurrent evolution of improved fishing techniques and gear modifications developed by NMFS and the tuna industry and increased awareness of the captain and crew of the necessity to reduce incidental porpoise mortality. The following general list summarizes the activities which allowed the low mortality rate.

1) Set positioning to minimize negative effects of wind and current.

2) Early recognition of potential net collapse areas and use of speedboat(s) to prevent collapse.

3) Use of speedboats to herd porpoise out of potential danger areas.

4) Use of speedboats to adjust backdown area corkline prior to backdown.

5) Consistent use of two or three speedboats at backdown apex to prevent fish loss and to rescue porpoise.

6) Consistent backing down until all live porpoise are out of the net (very important).

7) Use of person in inflatable raft to:

a) Signal when backdown apex is clear of fish;

b) herd and hold the porpoise in the backdown apex;

c) determine by using a mask and snorkel and by listening, when all live porpoise are out of the net; and

d) hand-releasing animals.

8) Incorporation of small-mesh, double-depth safety panel.

9) Incorporation of "super-apron."

MFR Paper 1251. From Marine Fisheries Review, *Vol. 39, No. 6, June 1977. Copies of this paper, in limited numbers, are available from D825, Technical Information Division, Environmental Science Information Center, NOAA, Washington, DC 20235. Copies of* Marine Fisheries Review *are available from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 for $1.10 each.*

7709

ANNUAL FLUCTUATIONS IN BIOMASS OF TAXONOMIC GROUPS OF ZOOPLANKTON IN THE CALIFORNIA CURRENT, 1955-59

J. M. COLEBROOK[1]

ABSTRACT

Year-to-year fluctuations in the abundance of the zooplankton of the California Current region, from 1955 to 1959, have been studied. The abundance of zooplankton was measured in terms of the biomass of each of 17 major taxonomic categories (generally Class or Order). Principal components analysis was used to produce concise descriptions of the major elements of the fluctuations in the abundance of the categories in each of 14 areal subdivisions of the survey area. Considerable coherence with respect to annual changes was found both between the taxonomic categories and between the areas. The principal common element in the fluctuations could be associated with a marked increase in the temperature of the surface waters which occurred in 1957 and persisted through 1958 and 1959. A less pronounced but still quite clear common element in the fluctuations could be associated with year-to-year fluctuations in the amount of coastal upwelling in the area.

Since 1949, the regular surveys conducted by the California Cooperative Oceanic Fisheries Investigation (CalCOFI) program have yielded information about a variety of physical, chemical, and biological parameters (see, e.g., Marine Research Committee 1957). For the CalCOFI survey cruises during January, April, July, and October for each of the years from 1955 to 1959, samples of zooplankton were analyzed to provide estimates of the biomass for each major taxonomic category within the zooplankton (Isaacs et al. 1969).

These data were generously made available to the author by J. D. Isaacs to provide material for a study of year-to-year changes in the abundance of the major components of the zooplankton. As stated by Isaacs et al. (1969), "Selection of the years 1955 through 1959 for analysis of biomass distribution was dictated by interest in the occurrence and nature of patterns of seasonal and annual variability among the functional groups of zooplankton. During this time, yearly mean temperatures above the thermocline shifted upward from the relatively cold years of 1955 and 1956 to the relatively warm years of 1958 and 1959."

The object of the study described in this paper is to describe the annual changes, from 1955 to 1959, in the abundance of the zooplankton of the CalCOFI survey area in as much detail as is available from the survey data in order to discover whether observed changes can be associated with environmental fluctuations.

MATERIAL

The details of the procedures for deriving biomass estimates have been described by Isaacs et al. (1969), who also give the reasons for the selection of the particular set of taxa (listed in Table 1). It was their intention to provide estimates of the "nutrient quality" of the standing crop of zooplankton as well as an index of "trophodynamic complexity." The categories were chosen to represent the quality and quantity of zooplankton as food for fish rather than as indicators of variability of the zooplankton as such.

TABLE 1.—A list of the taxa from CalCOFI cruises for which biomass estimates are available. They are listed in alphabetical order and a code used in Figures 7 and 10 is given.

Taxa	Code	Taxa	Code
Amphipoda	AMPH	Larvacea	LARV
Chaetognatha	CHET	Medusae	MEDS
Cladocera	CLAD	Mysidacea	MYSD
Copepoda	COPD	Ostracoda	OSTR
Crustacea larvae	CRST	Pteropoda	PTER
Ctenophora	CTEN	Radiolaria	RADL
Decapoda	DECP	Siphonophora	SIPH
Euphausiacea	EUPH	Thaliacea	THAL
Heteropoda	HETP		

The collection method for the standard CalCOFI plankton samples has been described in

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Manuscript accepted October 1976.

detail by, e.g., Ahlstrom (1954) and Fleminger (1964). Very briefly, the net is 1 m in diameter at the mouth and 5 m long, the filtering section having a mesh size of about 0.5 mm. The net is towed obliquely, from a ship traveling at a speed of about 2 knots, from the surface down to a depth of 140 m and then returned to the surface. The volume of water fitered varies from about 400 to 600 m^3.

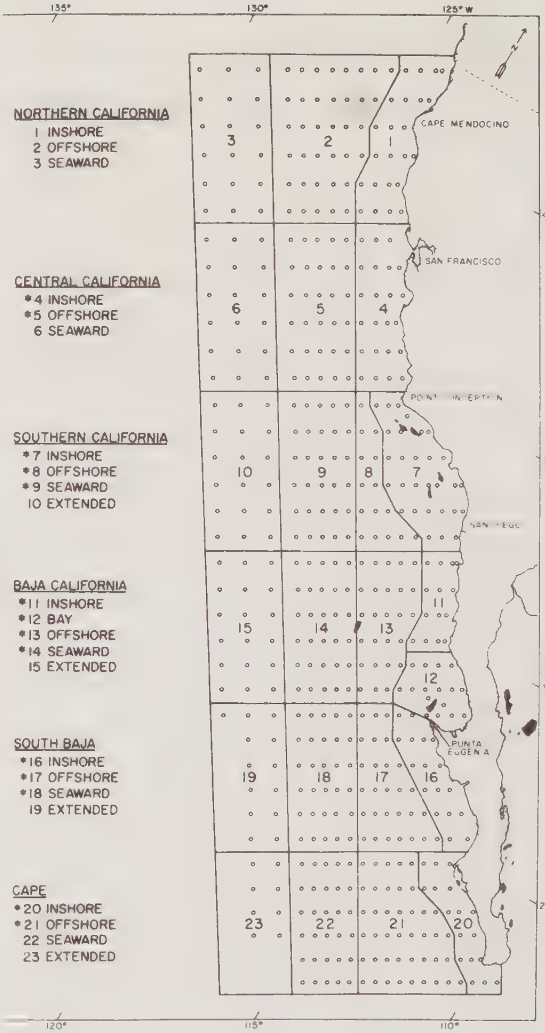
Charts of the distribution of biomass for each taxon have been given by Isaacs et al. (1969) for the April and October cruises, by Isaacs et al. (1971) for the January cruises, and by Fleminger et al. (1974) for the July cruises. The station data are held on a magnetic tape file at the Southwest Fisheries Center, National Marine Fisheries Service.

DATA PROCESSING METHODS

For the purposes of presenting summaries of CalCOFI data in a compact form and to permit some smoothing of the data by taking average values, P. E. Smith's proposal for subdividing the survey area into 23 zones was used in this study (Figure 1). The extent of the survey and hence the number of stations occupied varied from cruise to cruise. The station patterns for the cruises included in this study are given in Smith (1971), and a summary showing the numbers of samples in each zone is given in Table 2.

The biomass data are available as grams/1,000 m^3 and estimated to two decimal places. The range of estimates is from zero to over 5,000 g, and within each taxon they are heavily positively skewed.

The results presented here were expressed in terms of relative changes in biomass in time and space within each taxonomic category, and extensive averaging was employed. It was decided, therefore, to apply a logarithmic transformation to the original estimates. Averages based on log transformed values are weighted in favor of the more numerous low values as opposed to arithmetic means, the values of which may be determined largely by small numbers of high estimates.



135°
130°
125° W
NORTHERN CALIFORNIA
1 INSHORE
2 OFFSHORE
3 SEAWARD
CENTRAL CALIFORNIA
*4 INSHORE
*5 OFFSHORE
6 SEAWARD
SOUTHERN CALIFORNIA
*7 INSHORE
*8 OFFSHORE
*9 SEAWARD
10 EXTENDED
BAJA CALIFORNIA
*11 INSHORE
*12 BAY
*13 OFFSHORE
*14 SEAWARD
15 EXTENDED
SOUTH BAJA
*16 INSHORE
*17 OFFSHORE
*18 SEAWARD
19 EXTENDED
CAPE
*20 INSHORE
*21 OFFSHORE
22 SEAWARD
23 EXTENDED
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
CAPE MENDOCINO
40° N
SAN FRANCISCO
POINT CONCEPTION
35°
SAN DIEGO
30°
PUNTA EUGENIA
25°
120°
115°
110°

FIGURE 1.—A chart of the area of the CalCOFI survey showing the grid of station positions on which were based the cruises during the period 1955-59. Also shown is the subdivision of the area into the standard zones used in this study. The well-sampled zones for which annual means of biomass were calculated are marked with an asterisk (see Table 2).

In order to give zero a value on the transformed scale it is normal to add 1 to the observation prior to transformation. In this case, where the biomass has been estimated to two decimal places, a number of options is available, either 1.0, 0.1, or 0.01 can be added prior to transformation. Trials involving the calculation of means for each zone for each cruise for a subset of the taxonomic categories indicated that adding 1.0 produced a considerable loss of resolution for means corresponding to less than 1 g/1,000 m^3, and adding 0.01 produced a resolution of low means that appeared to be greater than was warranted by the accuracy of the data. Therefore throughout this study a transformation of the form

$$Y = \log_{10}(10X + 1)$$

TABLE 2.—The numbers of samples collected during each of the January (Jn), April (Ap), July (Jl), and October (Oc) CalCOFI cruises for the years 1955-59 in each of the standard zones (see Figure 1). Annual totals are given in boldface and the grand total is printed in italic.

	1955					1956					1957					1958					1959					
Zone	Jn	Ap	Jl	Oc	Total	Jn	Ap	Jl	Oc	Total	Jn	Ap	Jl	Oc	Total	Jn	Ap	Jl	Oc	Total	Jn	Ap	Jl	Oc	Total	Grand total
Central California:																										
Inshore	0	0	13	13	**26**	0	18	16	0	**34**	0	0	16	0	**16**	9	21	23	20	**73**	15	20	24	18	**77**	*226*
Offshore	0	0	9	6	**15**	0	9	18	0	**27**	0	0	10	0	**10**	2	21	20	17	**60**	12	14	30	18	**74**	*186*
Southern California:																										
Inshore	20	17	27	22	**86**	21	22	29	27	**99**	0	25	26	26	**77**	18	27	26	29	**100**	29	28	28	27	**112**	*474*
Offshore	4	6	14	6	**30**	4	6	13	9	**32**	0	7	12	6	**25**	5	13	14	9	**41**	6	12	14	9	**41**	*169*
Seaward	3	17	20	6	**46**	5	13	26	6	**55**	0	17	23	17	**57**	11	21	27	17	**76**	11	30	29	17	**87**	*321*
Baja California:																										
Inshore	12	12	13	12	**50**	12	12	14	0	**38**	8	13	12	13	**46**	12	13	11	13	**49**	13	14	13	14	**54**	*237*
Bay	12	13	14	11	**50**	11	12	15	0	**38**	12	15	16	14	**57**	10	16	14	16	**56**	15	16	17	16	**64**	*265*
Offshore	11	13	26	4	**54**	11	11	22	0	**44**	10	20	26	11	**67**	10	25	25	18	**78**	18	26	24	16	**87**	*330*
Seaward	4	12	24	5	**45**	6	16	20	0	**42**	2	16	19	13	**50**	10	30	23	18	**81**	18	29	29	18	**94**	*312*
South Baja:																										
Inshore	16	15	16	14	**61**	13	13	14	0	**40**	16	15	17	17	**65**	15	16	17	17	**65**	17	11	19	17	**64**	*295*
Offshore	8	12	13	6	**39**	8	8	13	0	**29**	8	21	18	12	**59**	12	22	19	20	**73**	19	17	27	20	**83**	*283*
Seaward	3	2	2	3	**10**	1	2	2	0	**5**	1	12	13	13	**39**	3	15	6	7	**31**	8	7	12	8	**35**	*120*
Cape:																										
Inshore	15	0	0	0	**15**	16	16	0	0	**32**	0	19	0	0	**19**	17	0	0	17	**34**	20	10	0	0	**30**	*130*
Offshore	1	0	0	0	**1**	1	10	0	0	**11**	0	22	0	0	**22**	10	0	0	24	**34**	31	14	0	0	**45**	*113*

has been employed. By this transformation, means corresponding to greater than about 0.2 g/1,000 m^3 are virtually on a logarithmic scale while lower means show a progressive transition to an arithmetic scale.

Quarterly means were calculated by averaging the data for the stations in each zone and then these were averaged to give annual values. For those occasions when less than five stations were occupied in any zone, the station data were ignored and a quarterly mean was interpolated by the following method:

1. For each taxonomic category the set of overall zone means (the sum of all the observations for all the cruises in each zone divided by the total number of stations occupied in the zone) was calculated. The set of overall quarterly means (the sum of all the observations for all the cruises in each quarter divided by the number of stations in each quarter) was calculated.
2. For each missing value the sum of the remaining means for the other zones for the cruise and the sum of the corresponding overall zone means were calculated. The latter was weighted by the ratio of the relevant overall quarterly mean to the grand mean and the missing value then calculated as the product of the remaining zone means for the cruise and the weighted sum of the overall zone means.

From these quarterly means, annual means were calculated for each taxon for each of a set of regularly sampled zones (those marked with an asterisk in Figure 1); and principal components analysis was used to extract from these data the main patterns of year-to-year change in biomass. This is a technique of multivariate analysis (see, e.g., Kendall 1957) which generates a sequence of variables known as components with, in this case, values for each year, which are the weighted sums of the standardized data variables, in this case sets of annual means of the taxonomic categories. The sets of weighting factors, with values for each taxonomic category, are the successive latent vectors of the correlation matrix derived from the original data, in this case the table of correlations between the annual variations in abundance of all possible pairs of taxonomic categories. The first latent vector generates a component which has the largest possible variance. The second vector generates a component which has the largest possible variance in relation to the residual following the removal of the variability associated with the first component, and so on. If the original data are coherent to any extent, it is normal for the first few components to account for a large proportion of the variability of the original data array.

GEOGRAPHICAL DISTRIBUTIONS

To provide some geographical background to the study of year-to-year changes in biomass, charts of the overall mean for each taxon in each standard zone were prepared. In order to search for possible relationships between the geographical distributions of the taxonomic categories, these data were subjected to a principal components analysis.

Figure 2 is a graph of the first latent vector plotted against the second. The graph has a point for each taxonomic category, and the disposition of points represents in a spatial form the relationships between the geographical distributions of the taxonomic categories with respect to the first two components which, in this case, account for 61% of the variability of the original geographical distributions. The interrelationships are probably best regarded in the form of a more or less circular sequence; only the point for Medusae falls well off the sequence.

Figure 3 shows charts of the first two components. The first component shows a very clear north to south, alongshore gradient; and the second shows an equally clear inshore to offshore gradient, indicating that the sequence of categories in Figure 2 runs from categories with northern distributions (Siphonophora to Radiolaria) to inshore distributions (Euphausiacea to Cladocera) to southern and inshore distributions (Larvacea to Mysidacea) to offshore distributions (Heteropoda to Ostracoda). Figure 4 shows the distributions of the taxonomic categories arranged in this sequence. They are based on averages of the transformed data, for each zone, for each quarterly cruise for the period 1955-59, excluding zones for which fewer than five stations were occupied. These distributions show variability other than that involved in their relationships with the first two components; nevertheless, the north to inshore to south to offshore sequence can be seen fairly clearly. Heteropods and Pteropods are firmly placed in the sequence of taxonomic categories in the vector plot in Figure 2. They have, however, fairly low values compared with the other categories, and only parts of their distributions conform with the south to offshore transition indicated by their position in the vector plot. The distribution of Medusae (Figure 4) can be seen to include areas of relatively high biomass both in the north and in the south, and clearly it does not fit into the sequence of the other categories.

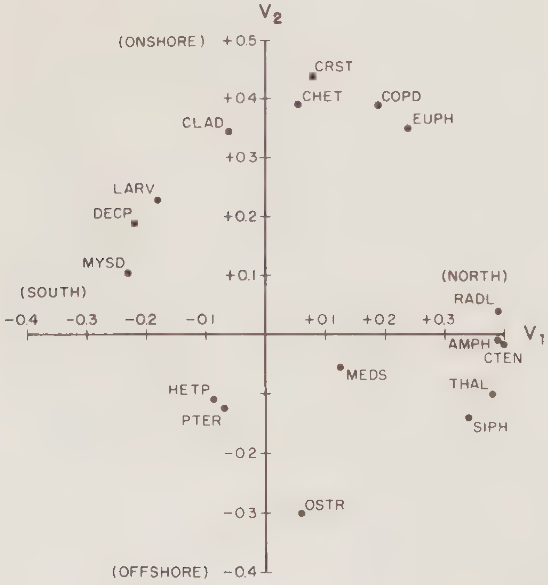


FIGURE 2.—A plot of the first vector against the second vector derived from a principal components analysis of the geographical distributions of the taxa. A key to the abbreviations of the names of the categories is given in Table 1.

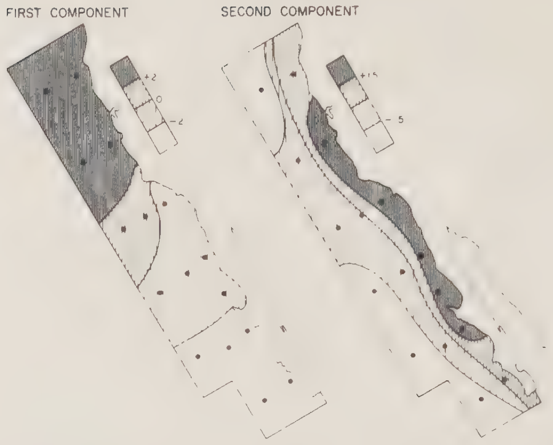


FIGURE 3.—Charts of the first and second components derived from a principal components analysis of the geographical distributions of the taxa.

It is obviously unrealistic to attempt to classify the internally diverse taxonomic categories used here in terms of geographical distribution types such as Brinton (1962) found for Euphausiacea. Brinton found that the alongshore axis of the California Current in the CalCOFI survey area was characterized by transitions from "subarctic" species in the north to "transition" species in the region between lat. 30° and 40°N to "equatorial" species in the south. "Central" species occurred offshore and some "boundary" species occurred inshore in the area. McGowan (1971) has shown that these patterns are reflected generally in the distribution of the plankton of the Pacific Ocean. It may, nevertheless, be significant that the pattern of distribution of the taxonomic categories reflects both the alongshore and the inshore-offshore transitions in the distribution of the Euphausiacea.

YEAR-TO-YEAR FLUCTUATIONS IN BIOMASS

Annual means of biomass were calculated, as described above, for each taxonomic category (Table 1) for each of the well-sampled standard zones (Figure 1) for each of the years 1955-59. Two sets of principal components analyses were carried out, firstly for each of the 14 standard zones on the annual fluctuations in biomass of each taxonomic category and secondly for each taxonomic category on the annual fluctuations in abundance in each of the standard zones. The same data are involved in both sets of analyses.

Graphs of the first principal components for each of the zone analyses are given in Figure 5. Table 3 shows that these components accounted for between just under one-half and about three-quarters of the total variability; it also shows that all but a very few of the categories showed positive relationships with the components. The graphs show considerable similarity between the various zones. These results indicate that a large element of the year-to-year fluctuation in biomass is common to all the zones and to a vast majority of the taxonomic categories. Nearly all the zones show a relatively high biomass (relative to a mean of zero) in 1955 and 1956 and a low biomass in 1958 and 1959. The data for 1957 vary from zone to zone, perhaps tending to be higher in the northern and offshore zones and lower in some of the southern and inshore zones.

A table was prepared of the corresponding vectors with the taxonomic categories arranged, by trial and error, to give the high positive terms at the top, and the low positive and the few negative terms at the bottom of the table. The final ranking of categories and the vector values are given in Table 4. This rank was compared with the rank of taxa based on the relationships between their geographical distributions (Figure 2) starting with the northern distributions, with Siphonophora and Thaliacea, working round the sequence and ignoring Medusae (also left out of Table 4) to finish with Pteropoda and Ostracoda.

TABLE 3.—For each zone (*a*) the percentage of the total variability of the original data accounted for by the first component and (*b*) the number of taxa with positive first vector values (maximum = 17). The code names for the zones used in Table 4 and Figures 6 and 9 are also given.

Zone	Code	*a*	*b*
Central California:			
Inshore	CCALIN	74	17
Offshore	CCALOF	71	17
Southern California:			
Inshore	SCALIN	63	14
Offshore	SCALOF	58	17
Seaward	SCALSW	58	15
Baja California			
Inshore	BCALIN	70	15
Bay	BCALBY	66	16
Offshore	BCALOF	52	14
Seaward	BCALSW	48	13
South Baja:			
Inshore	SBAJIN	64	16
Offshore	SBAJOF	56	16
Seaward	SBAJSW	45	12
Cape:			
Inshore	CAPEIN	54	15
Offshore	CAPEOF	53	16

TABLE 4.—The first vectors of principal component analyses for each standard zone with the taxonomic categories ranked as described in the text. Also the rank of the categories derived from Figure 2.

Taxa	CCALIN	CCALOF	SCALIN	SCALOF	SCALSW	BCALIN	BCALBY	BCALOF	BCALSW	SBAJIN	SBAJOF	SBAJSW	CAPEIN	CAPEOF	"Atlas" rank
Copepoda	0.28	0.28	0.30	0.31	0.36	0.29	0.29	0.30	0.34	0.30	0.30	0.31	0.27	0.30	7
Thaliacea	0.27	0.27	0.30	0.28	0.31	0.28	0.29	0.32	0.33	0.29	0.31	0.29	0.30	0.31	2
Amphipoda	0.27	0.28	0.30	0.32	0.31	0.27	0.28	0.31	0.33	0.28	0.28	0.22	0.29	0.28	4
Siphonophora	0.27	0.28	0.22	0.29	0.23	0.29	0.29	0.25	0.29	0.28	0.30	0.32	0.28	0.28	1
Radiolaria	0.28	0.27	0.30	0.29	0.31	0.28	0.28	0.30	0.28	0.23	0.28	0.20	.02	0.00	5
Ctenophora	0.26	0.27	0.30	0.26	0.28	0.26	0.26	0.26	0.33	0.27	0.26	0.06	0.16	0.05	3
Decapoda	0.25	0.25	0.26	0.29	0.29	0.27	0.24	0.31	0.29	0.24	0.28	0.29	0.30	0.33	12
Euphausiacea	0.27	0.26	0.28	0.26	0.26	0.28	0.21	0.14	0.17	0.24	0.28	0.18	0.18	0.31	6
Chaetognatha	0.28	0.27	0.30	0.28	0.28	0.27	0.24	0.11	0.27	0.24	0.25	.26	0.31	0.32	9
Crustacea larvae	0.25	0.06	0.30	0.27	0.22	0.25	0.24	0.17	.09	0.25	0.31	.25	0.29	0.11	8
Heteropoda	0.15	0.24	0.14	0.18	0.23	0.16	0.29	0.20	0.07	0.19	0.29	0.19	0.27	0.28	14
Larvacea	0.28	0.27	0.17	0.13	0.24	0.27	0.29	0.21	.05	0.22	.08	0.29	0.22	0.23	11
Ostracoda	0.22	0.26	.01	0.26	0.23	0.12	0.18	0.23	0.13	0.18	0.11	.21	0.21	0.24	16
Cladocera	0.12	0.19	.03	0.01	0.03	.23	0.03	.25	0.06	0.23	0.17	0.11	0.09	.08	10
Pteropoda	0.19	0.13	0.10	0.08	.02	0.04	0.12	.02	.19	.06	0.05	.08	.17	0.21	15
Mysidacea	0.15	0.17	.28	0.09	.15	0.08	0.11	.12	.27	0.26	0.14	.33	0.29	0.16	13

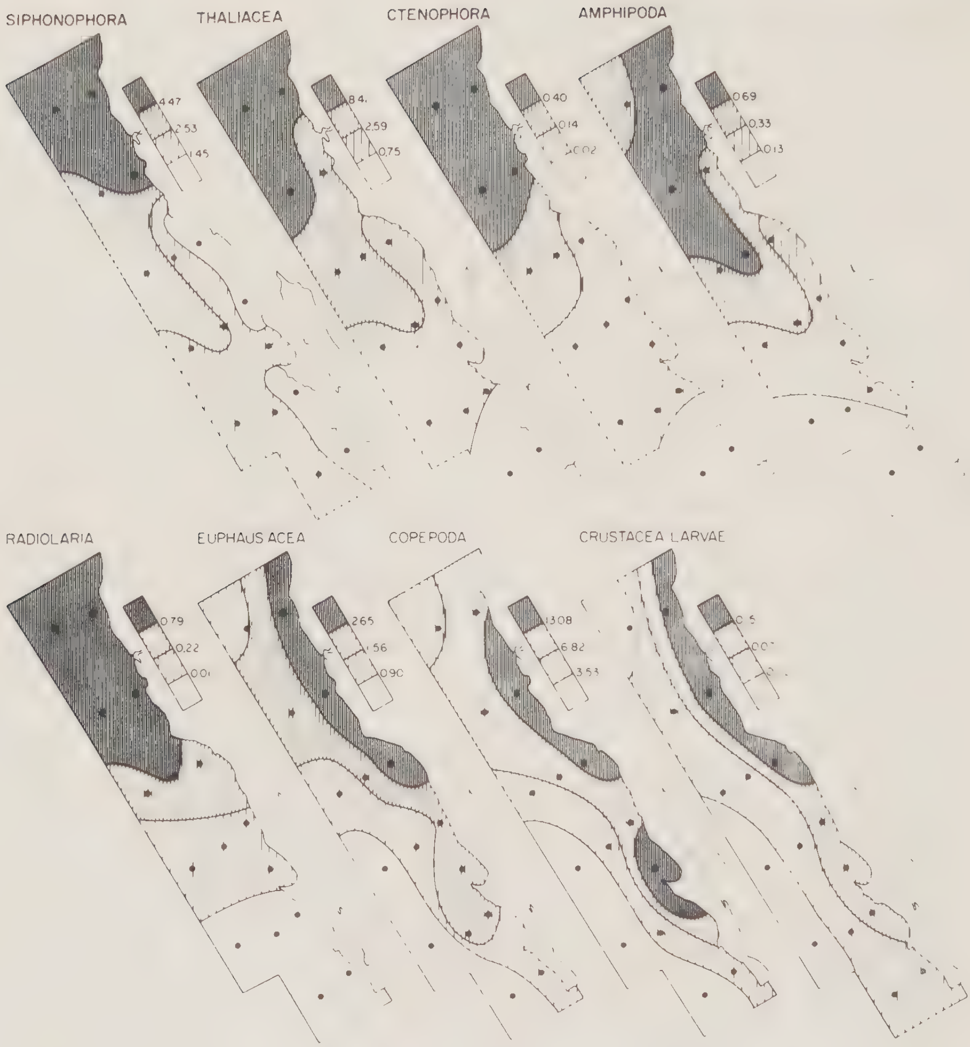

SIPHONOPHORA
4.47
2.53
1.45
THALIACEA
8.4
2.59
0.75
CTENOPHORA
0.40
0.14
0.02
AMPHIPODA
0.69
0.33
0.13
RADIOLARIA
0.79
0.22
0.01
EUPHAUSACEA
2.65
1.56
0.90
COPEPODA
13.08
6.82
3.53
CRUSTACEA LARVAE

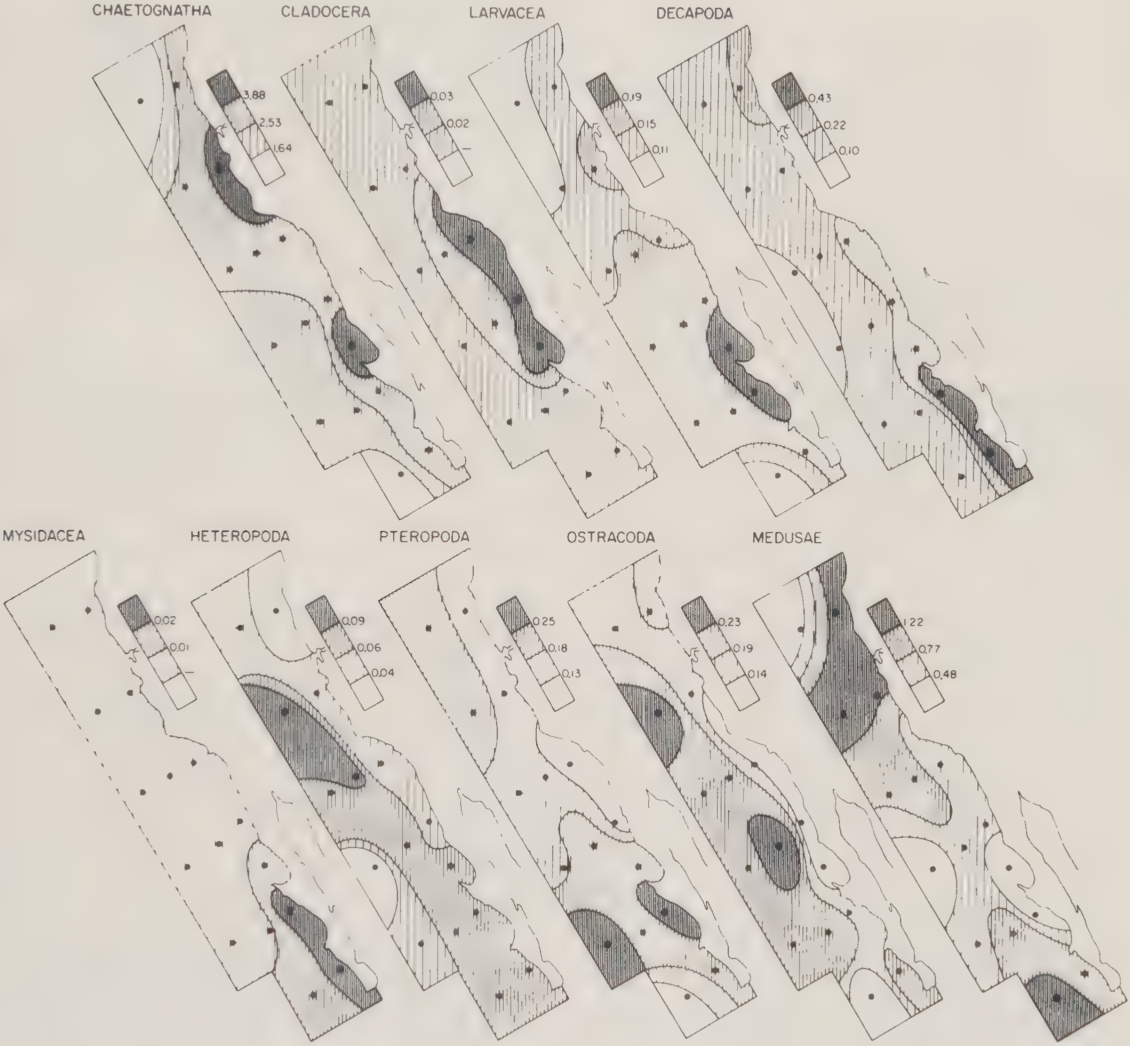
FIGURE 4.—Charts of the geographical distribution of biomass for each of the taxa based on logarithmic means for each standard zone (see Figure 1) for all the CalCOFI cruises for 1955-59. Contours are drawn at levels correspond-

The ranks are given in Table 4, and the value of Spearman's rank correlation coefficient between the two ranks is +0.806 which is significant at the 0.1% level.

Figure 6 shows graphs of the first principal components of the analyses for each taxonomic category with the categories ranked in the same order as in Table 4. All the northern and inshore categories, down to Crustacea larvae in Figure 2, show the same form of year-to-year fluctuations in biomass as do the zones, with relatively high biomass in 1955 and 1956 and low biomass in 1958 and 1959. The remaining categories show some features of this pattern with only Cladocera showing a negative relationship.

These results suggest that whatever influence or influences are responsible for the fluctuations in the plankton either have their origin in the north of the survey area or have a greater effect on those categories with northern patterns of distribution. It is, at least, fairly safe to infer that there is some commonality between the influences which determine geographical distribution and those which are responsible for the form of the year-to-year changes in biomass.

The years from 1955 to 1959 were deliberately


CHAETOGNATHA
3.88
2.53
1.64
CLADOCERA
0.03
0.02
LARVACEA
0.19
0.15
0.11
DECAPODA
0.43
0.22
0.10
MYSIDACEA
0.02
0.01
HETEROPODA
0.09
0.06
0.04
PTEROPODA
0.25
0.18
0.13
OSTRACODA
0.23
0.19
0.14
MEDUSAE
1.22
0.77
0.48

ing to the mean + 1 SD, the mean, and the mean − 1 SD. The keys to the contour levels for each category give the arithmetic values, as grams per 1,000 m^3, corresponding to these levels.

chosen for the production of biomass data to cover a period of marked change in physical conditions and in the distribution of many species in the CalCOFI area. The main features of these changes have been described in the proceedings of a special symposium (Sette and Isaacs 1960). The most striking feature was a considerable warming of the surface waters which started in the south in 1956 and spread through the area during 1957 (see, e.g., Longhurst 1967).

The general form of the change can be typified by the variation in temperature in the top 50 m in the southern California offshore area shown in Figure 7. Favorite and McLain (1973) showed that this is part of a widespread change in surface temperature affecting almost the whole of the North Pacific Ocean. The reasons for the change are not yet completely clear. The initial warming in 1957 appears to be associated with a reduction in the flow of the California Current which occurred between the late summer of 1957 and midsummer 1958. As an index of the flow of the California Current, Saur (1972) used the difference in sea level between Honolulu and San Francisco. A plot of monthly means (with a linear trend removed and adjusted to normal atmo-

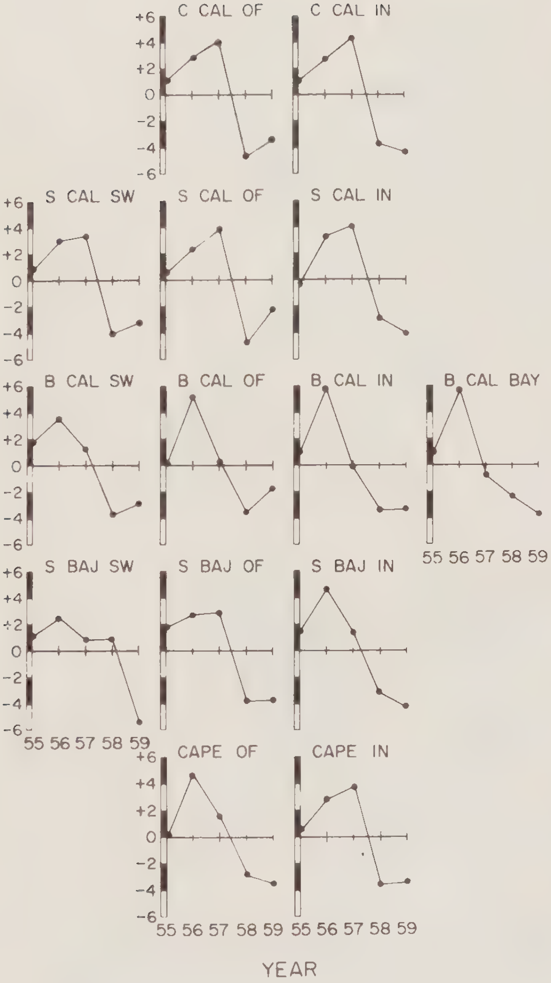


FIGURE 5.—Graphs for each of the well-sampled CalCOFI zones (see Figure 1) of the first principal component of the year-to-year fluctuations in biomass of all the 17 taxa. Each graph is drawn with a mean of zero and the vertical scale is in SD units.

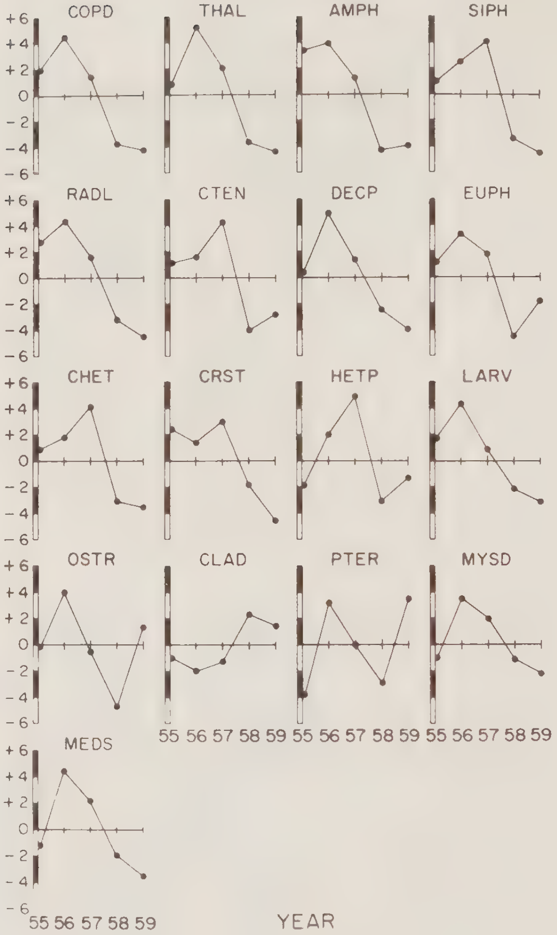


FIGURE 6.—Graphs for each taxon of the first principal component of the year-to-year fluctuations in biomass for all the well-sampled CalCOFI standard zones. A key to the abbreviations of the names of the taxa is given in Table 1. They are in the same order as in Table 4 (see text). Each graph has a mean of zero and the vertical scale is in SD units.

spheric pressure) for 1955-59 is shown in Figure 7. Differences greater than 58 cm are believed to indicate a stronger than normal flow and differences less than 58 cm a less than normal flow. It can be seen that the period of less than normal flow in 1957-58 corresponds well with the timing of the increase in temperature in the southern California offshore zone. In the California Current region, and indeed over most of the eastern North Pacific, the increase in temperature persisted through 1958 and 1959 while the sea level differences indicate a normal or above average flow during this time. The period of below normal flow corresponds with El Niño off the coast of Peru and perhaps with an anomalous weakening of the trade winds of the southern hemisphere and a concurrent reduction of equatorial upwelling (Bjerknes 1966; Favorite and McLain 1973).

Wickett (1967) found a relationship between the year-to-year changes in zooplankton volume for the CalCOFI survey (Thrailkill 1963) and the mean meridional Ekman transport (Fofonoff 1962) for January to August in the previous year at lat. 50°N, long. 140°W (over 1,000 miles upstream from the CalCOFI survey area) for the years 1952-59. He suggested that a major cause of variation in the abundance of zooplankton in the California Current region is the change in the

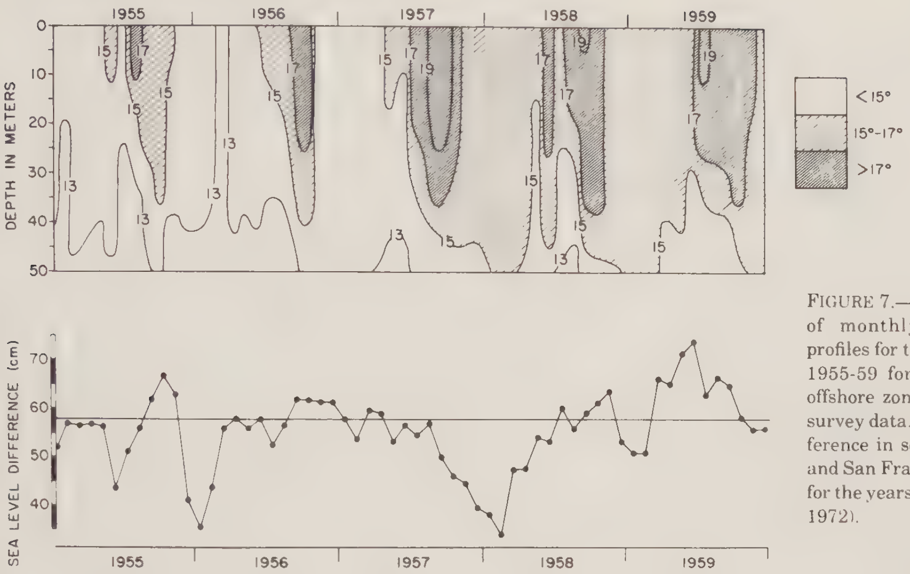


FIGURE 7.—Top) A contoured diagram of monthly vertical temperature profiles for the upper 50 m for the years 1955-59 for the southern California offshore zone (see Figure 1). CalCOFI survey data. Bottom) A graph of the difference in sea level between Honolulu and San Francisco at monthly intervals for the years 1955-59 (plotted from Saur 1972).

proportion of the superficial wind-driven water that is swept southward out of the North Pacific subarctic circulation.

There seems little doubt that the change in temperature in 1957 and its persistence through 1958 and 1959 is related to the relative reduction in biomass of the zooplankton associated with the first principal components of all zones and most of the taxonomic categories. The data presented by Wickett showed a marked reduction in southward transport at lat. 50 N, long. 140°W during 1958 and 1959 and this, coupled with the reduction in the flow of the California Current in 1957 and 1958 (Figure 7), would appear to support Wickett's suggestion of a direct influence by water movements. The relationship between the north to south geographical gradient (Figure 3) and the first principal components is also entirely consistent with this hypothesis.

An examination of the remaining components for each of the zones indicated the existence of a second pattern of fluctuation common to most of the zones. In Figure 8 are given graphs of a component, other than the first, for each zone selected to give the best approximation to a form common to all the zones. In 8 of the 14 zones it is the second component; in the remaining zones it is either the third or the fourth component. Given the quantity and the quality of the original data and considering the large proportion of the variability of the data associated with the first components, the lack of consistency in the position of the common pattern among the components is perhaps not surprising. Figure 9 shows the same for each taxonomic category; again the majority are second components and only one, for Radiolaria, is the fourth component. The main features of the pattern are a low in 1957 and highs in 1956 and 1958; 1955 and 1959 tend to be low but their positions vary somewhat within both the zones and the taxonomic categories.

Coastal upwelling is a feature of the California Current region, and Bakun (1973) has produced estimates of relative fluctuations in upwelling at a number of positions along the west coast of North America. They are based on estimates of the offshore component of the Ekman transport which is in turn estimated from atmospheric pressure fields.

Monthly means of the upwelling index for five positions off the coast at latitude and longitude 36°N, 122°W; 33°N, 119°W; 30°N, 116°W; 27°N, 116°W; and 24°N, 113°W, for the period 1955-58 were extracted from Bakun's report. Uncertainties about the differences in absolute terms between the estimates at different positions particularly off southern California, discussed by Bakun, suggested that principal components might provide a good method of summarizing the data from this set of positions. For each calendar month, analyses were carried out on the index estimates for the five positions and the 5 yr. Examination of the components showed that a pattern common to the first 7 mo of the year was

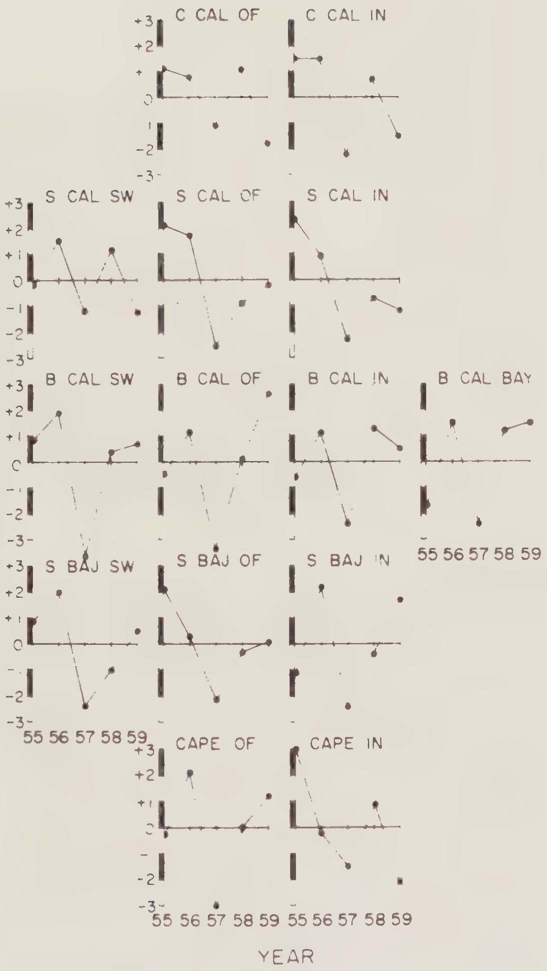


FIGURE 8.—Graphs, for each CalCOFI standard zone, of principal components of annual fluctuations in biomass. See text for the method of selection of the components, see also the legend to Figure 6

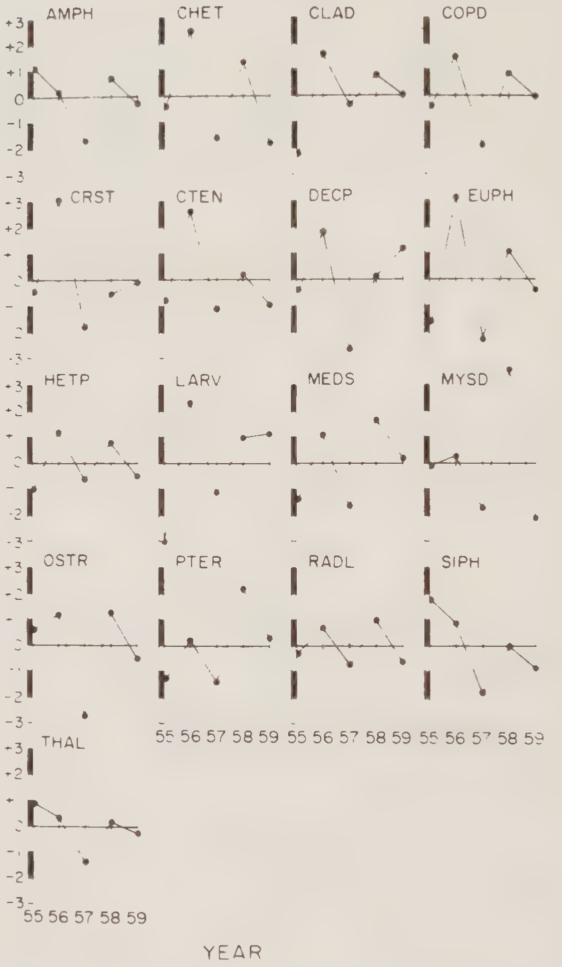


FIGURE 9.—Graphs, for each taxonomic group (Table 1), of principal components of annual fluctuations in biomass. See text for the method of selection of the components, see also the legend to Figure 7

present within the components, and graphs of these are given in Figure 10. The pattern was found as the first component in all the months except March and April where it was found in the second component. Graphs of the first components for August to December are also given in Figure 10.

There is a marked similarity between the pattern of year-to-year fluctuations in upwelling as represented by the components for the first 7 mo of each year and the fluctuations in biomass of the zooplankton represented by the components shown in Figures 8 and 9, and it is reasonable to assume that some form of causal relationship is involved. As with the first component in relation to the temperature range, the precise mechanisms involved cannot be inferred from the information here. Upwelling has effects on the vertical temperature structure and particularly on the timing of the establishment of a clear thermocline. It can also be expected to have a considerable influence on the supply of nutrients. It is probable, therefore, that the effect on the zooplankton is an indirect one through the influence of vertical stability of the water column and the supply of nutrients on primary production processes. Peterson (1973) has established a relationship between year-to-year variation in upwelling

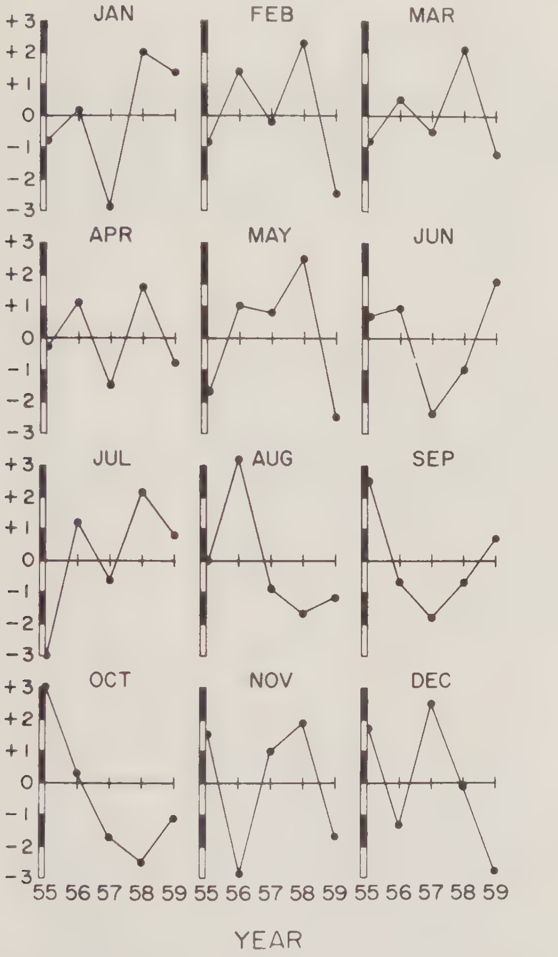


FIGURE 10.—Graphs of principal components of upwelling index for the CalCOFI survey area for each month for the years 1955-59. See text and Bakun (1973).

off the coast of Oregon and the catch of the Dungeness crab, *Cancer magister*, with a time lag of about 18 mo. He attributed this to an increased food supply in years with pronounced upwelling, implying a relationship between upwelling and plankton similar in sign to that found further south in the California Current.

CONCLUSIONS

At least during the period 1955-59, a considerable proportion of the variability from year to year in the biomass of zooplankton, as represented by estimates for the taxa listed in Table 1, can be associated with hydrographic events, variations in the strength of the California Current, and variations in the intensity of coastal upwelling. The precise mechanisms involved are not clear, but in relation to the California Current there is a similarity in the relationships within the taxa with respect to both geographical distribution and annual fluctuations in abundance which suggests that advection of stocks may be involved to a considerable extent. The influence of upwelling on primary production through effects on temperature stratification and the supply of nutrients probably accounts for the relationship with the zooplankton.

The only data that have been produced routinely from the whole series of CalCOFI cruises, which relate to plankton other than fish eggs and larvae, are in the form of displacement volumes of unsorted samples (Smith 1971). The marked coherence between the various taxonomic categories suggests that these data can be expected to produce estimates of long-term variations which indicate real changes in the abundance of the zooplankton. Such data cannot, however, reflect the geographical differentiation within the zooplankton, and this imposes a limit, to the extent to which they can be used, to provide the basis for the examination of the influences of a complex of environmental factors of the kind suggested by this study as playing an important role in determining the year-to-year fluctuations in the plankton.

The taxonomic categories used in this study were selected by Isaacs et al. (1969) to represent the plankton as food for fish. I have used them to represent fluctuations in the zooplankton as such for the 1955-59 period.

For future studies the only definitive method of selecting taxa to represent year-to-year changes in the zooplankton is by trial and error: there are, moreover, numerous possibilities, and the labor involved would be prohibitive if some compromise is not made. It is indicated above that there is a tendency for taxa which have similar geographical distributions also to show similar year-to-year fluctuations in abundance. As a first approximation, this fact might be used as a guide to the selection of representative categories. It is implicit that each selected category should be geographically homogeneous, and the set of categories should cover the full range of geographical distributions.

It is probable that the species is the highest taxon for which geographical homogeneity can be assumed, and even here there may be some species which have geographically differentiated races. Isaacs et al. (1969) gave an estimate of about 550 species found, or likely to be found, in the zooplankton of the CalCOFI survey area. Allowing for the fact that somewhere between one-half and three-quarters of these species will probably occur infrequently in samples, the labor involved in routinely analyzing for this number of species is very considerable. The geographical distributions of species belonging to many of the major taxa within the zooplankton have been studied and published in the CalCOFI Atlas series which could provide the basis for the selection of a limited number of species which will represent the range of geographical distributions in the survey area and, hopefully, will provide a good representation of the range of year-to-year fluctuations in abundance.

ACKNOWLEDGMENTS

My thanks are due to Brian Rothschild, Director, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, for making available to me the facilities of the La Jolla Laboratory. I also thank J. D. Isaacs for furnishing unpublished data. Nancy Wiley and Dorothy Roll were of great assistance in the computations involved in the study and John G. Wyllie helped with some data problems. Finally I must thank Paul E. Smith whose knowledge of the California Current region and of the CalCOFI survey was invaluable. My visit to the La Jolla Laboratory was supported by the U.K. Natural Environment Research Council.

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A Commercial Tilapia, *Tilapia mossambica*, Hatchery for Hawaiian Skipjack Tuna, *Katsuwonus pelamis*, Fishery—Cost Analysis and Problematical Study

BRUCE L. CRUMLEY[1]

ABSTRACT

The Hawaiian skipjack tuna fisherman spends a good part of his time catching nehu, *Stolephorus purpureus*, for bait instead of fishing. This paper considers pond-raised tilapia, *Tilapia mossambica*, as a possible alternative bait, and sets forth information about a commercial tilapia production plant. If the fishermen purchased tilapia and fished full time, their bait would cost less than it does now, since the current break-even cost to the fisherman of a bucket of nehu is determined to be $30.12, while the highest cost estimate for pond-reared tilapia is $17.56.

The catch rates for tuna when using nehu and tilapia as bait were studied, and found to be comparable. Tilapia still need extensive trials as a bait species, however, and tilapia data need further scrutiny.

Tilapia characteristics, both favorable and unfavorable, are discussed and should offer some insight into the problems and advantages of raising tilapia. The possibility of sharing the tilapia tanks with a compatible, marketable species, and thereby helping to defray expenses, are also discussed.

Fish diseases contracted during three different baitfish rearing studies are reviewed, along with their treatments.

INTRODUCTION

This paper sets forth information about a commercial tilapia, *Tilapia mossambica*, production plant, as far as what must be known and considered prior to the actual investment of cash. I investigated this subject as though this tilapia plant were being directed primarily to furnish tilapia for the local Hawaiian skipjack tuna, *Katsuwonus pelamis*, industry, although at the end of this paper I discuss possible alternative markets for tilapia and alternate uses of the production plant.

I began by studying the economic feasibility of such a production plant. Obviously, the figures used here will not apply in the future because of expected changes in price factors, but they provide a basis from which any interested individual or firm can derive information needed in considering such a commercial enterprise. I also discuss differences between the currently used baitfish, nehu, *Stolephorus purpureus*, and tilapia, and examine their relative efficiencies as skipjack tuna live bait.

I discuss the type of tank construction which has been used in the past and pointed out ways to facilitate such a plant's operation.

BACKGROUND

The Hawaiian skipjack tuna fishery is a live-bait fishery with an average annual ex-vessel value in excess of $2 million. Annual landings average over 4 million kg (9 million lb), but fluctuate between 2 and 7 million kg (5 and 16 million lb). This fluctuation is primarily due to:

1) availability of bait,
2) fragility of the bait, and
3) abundance and availability of the skipjack tuna.[2]

A possible solution to the problem of obtaining an adequate and dependable supply of baitfish would be for the fishermen to purchase bait, and to replace the time spent fishing for it ("baiting time") with time devoted entirely to fishing for aku ("fishing time"). This additional fishing time could increase the annual catch by as much as 66% and provide an increase in ex-vessel value of the catch by $1.9 million. This increase could occur with the existing fleet. Any growth of the fleet would result in an accompanying increase in ex-vessel value, since the skipjack tuna is underutilized (see footnote 2).

The problem then, is to estimate the indirect cost that the fisherman is incurring and the amount of skipjack tuna he is not catching because of the time he is spending baiting. This will give the estimated maximum cost per bucket that the fisherman should be willing to pay for bait. Obviously, this assumes that he will buy bait offered at a price that is less than the cost he is incurring by catching the bait himself. Past experience has shown this not to be the case. In the future, however, increasing

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[1] Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

[2] U.S. National Marine Fisheries Service. 1973. The tuna baitfish problem of Hawaii—an assessment and development of an action program. Unpubl. rep. prepared by Staff, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, HI 96812, 33 p.

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pressure may be exerted upon the fisherman to use his time more efficiently, abandoning the less efficient "traditional" ways that have hindered expansion of the commercial aku industry. This pressure could come from:

1) changing fleet composition, with more modern vessels in the *Anela*[3] class being added, permitting longer trips and travel to better fishing grounds during the off-season (October-April) and, at the same time, increasing the demand for live bait; and
2) increased world demand for high protein foods arising from a rapidly increasing population.

It is to the advantage of this study that the *Anela* has worked with different types of baitfish. This could serve to encourage other fishermen to use species other than the nehu.

One additional point is that the crew size could be reduced without the need for added crew members to bait (see footnote 2).

I have employed the approach used by Shang and Iversen (1971) to determine the indirect cost of baitfish to the fishermen, relying heavily upon Hida et al. (1962) for their statistics. Previously unpublished data gathered by the State Fish and Game Division at the Honolulu Bait Station (HBS) were used in a present-day cost estimate for a commercial tilapia production facility.

AN ESTIMATE OF THE VALUE OF NEHU

A good cost estimate at today's market prices is of prime importance in considering a commercial tilapia production plant. The cost estimate obtained in this paper is derived from prices effective as of 1 January 1974.

To determine the cost of nehu, the same problems present themselves here as they did to Shang and Iversen (1971), those of a vertically integrated system for fishing. Since no market exists for bait, the cost of nehu has been determined indirectly.

I have described an operation similar to that set forth in Shang and Iversen (1971) with 1973 prices for fuel, ice, and total catch. Because final figures are not yet available for the total days fished and days baited, certain assumptions must be made. Using Shang and Iversen's table 2, but with the new prices substituted:

Cost of Fishing and Baiting Per Trip

	Fishing	Baiting
Hours of operation[a]	14	3-h day baiting 5-h traveling
Fuel consumption (gal/h)	12.5	5 gal/h during baiting 12.5 gal/h during traveling
Price of fuel per gallon	$ 0.215	$ 0.215
Price of ice	$17.50	—
Total cost[b]	$55.12[c]	$16.66[d]

a. Fishing: 10-h scouting-fishing and 4-h traveling time (both ways).
Baiting: 5-h traveling—about 2 h to Pearl Harbor, 8 h to Kaneohe Bay (both ways).

b. Baiting trip uses less time than fishing trip and allows for more leisure time. The value of leisure time of fishermen is not incorporated in the calculation.

c. (14 × 12.5 × $0.215) + $17.50 = $55.12.

d. (3 × 5 × $0.215) + (5 × 12.5 × $0.215) = $16.66.

This shows that a fishing trip costs $38.46 more than a baiting trip. This must be taken into account when one is talking of increasing fishing time and reducing baiting time.

Referring to Table 1 we can see that the total skipjack tuna catch (in metric tons) did not vary much between 1972 and 1973. Ths actual day-baiting effort and actual days fished were assumed to remain relatively constant for these 2 yr, since the 1973 data for these two areas were not yet available. Shown are the effects of reductions in baiting effort by the amounts of 25%, 50%, 75%, and 100%.

Table 2 shows the number of buckets of nehu caught during day and night baiting. Since the number of buckets of bait caught in 1971 and 1972 did not fluctuate appreciably, an average for these 2 yr was used to estimate the number of buckets of bait caught in 1973.

38,786 buckets
36,713 buckets
75,499 buckets

$$\frac{75{,}499 \text{ buckets}}{2} = 37{,}748 \text{ buckets of bait}$$

Using Shang and Iversen's (1971) formulas:

$$C_0 = \left(\frac{D_b}{D_f}\right)V - (D_b \cdot C_d) \text{ and}$$

$$B_t = B_0 + B_a$$

$$\text{where } B_a = \frac{Q_a}{Q_b} = Q_a \cdot \left(\frac{B_0}{Q_t}\right)$$

and taking the values from Tables 1 and 2, the net opportunity costs (C_0) and the total amount of bait required (B') (in buckets) were obtained. Dividing C_0 by B_t gives the break-even price of nehu.

$$C_0 = \$1{,}974{,}673{,}698$$
$$B_t = 65{,}671 \text{ buckets.}$$

The break-even price is $30.12 per bucket of bait. (See p. 145, for calculations.)

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[3] The *Anela*, a 26.6-m steel vessel, joined the Hawaiian skipjack tuna fishing fleet in December 1971. Unlike the remainder of the skipjack tuna fleet (about 12 vessels), which consists of boats 17.8 to 24.5 m long with a bait-carrying capacity of only about 35 buckets, the *Anela* is capable of carrying 130 buckets. The *Anela* also has greater fish-carrying capacity and greater range, and represents a new look in the Hawaiian skipjack tuna fishery.

Table 1.—The actual and projected catch and value of skipjack tuna derived by reducing day-baiting effort by 25%, 50%, 75%, and 100%, 1965-72.

Year	Actual day-baiting effort	Actual days fished	Skipjack catch	Value	Catch per day fished	Price per ton	Reduction in day baiting	Reduction in day-baiting effort	Projected days fished	Projected skipjack catch	Projected value	Increase in catch	Increase in value
	No. of days	*No. of days*	*Metric ton*	*Dollar*	*Metric ton*	*Dollar*	*Percent*	*No. of days*	*No. of days*	*Metric ton*	*Dollar*	*Percent*	*Dollar*
1965	838	2,400	7,328.96	2,013,861	3.05	274.78	25	210	2,610	7,960.50	2,187,386	9	175,525
1966	781	2,086	4,256.82	1,403,623	2.04	329.74	25	195	2,281	4,653.24	1,534,359	9	130,736
1967	736	2,010	3,646.80	1,263,116	1.81	346.36	25	184	2,194	3,971.14	1,375,444	9	112,328
1968	1,055	2,177	4,227.41	1,539,617	1.94	364.20	25	264	2,441	4,735.54	1,724,684	12	185,067
1969	864	1,743	2,704.94	1,245,204	1.55	460.34	25	216	1,959	3,036.45	1,397,799	12	152,595
1970	1,017	1,894	3,334.46	1,496,919	1.76	448.92	25	254	2,148	3,780.48	1,697,133	13	200,214
1971	1,334	2,013	6,051.39	2,752,710	3.01	454.89	25	334	2,347	7,064.47	3,213,557	17	460,847
1972	1,187	1,882	4,952.12	2,949,372	2.63	595.58	25	297	2,179	5,730.77	3,413,132	16	463,760
1973	1,187	1,882	4,877.00	3,203,246	2.59	656.84	25	297	2,179	5,643.61	3,706,949	16	503,540
1965	838	2,400	7,328.96	2,013,861	3.05	274.78	50	419	2,819	8,597.95	2,362,545	17	348,684
1966	781	2,086	4,256.82	1,403,623	2.04	329.74	50	390	2,476	5,051.04	1,665,530	19	261,907
1967	736	2,010	3,646.80	1,263,116	1.81	346.36	50	368	2,378	4,304.18	1,490,796	18	227,680
1968	1,055	2,177	4,227.41	1,539,617	1.94	364.20	50	528	2,705	5,247.70	1,911,212	24	371,595
1969	864	1,743	2,704.94	1,245,204	1.55	460.34	50	432	2,175	3,371.25	1,551,921	25	306,717
1970	1,017	1,894	3,334.46	1,496,919	1.76	448.92	50	508	2,402	4,227.52	1,897,818	27	400,899
1971	1,334	2,013	6,051.39	2,752,710	3.01	454.89	50	667	2,680	8,066.80	3,669,507	33	916,797
1972	1,187	1,882	4,952.12	2,949,372	2.63	595.58	50	594	2,476	6,511.88	3,878,345	31	928,973
1973	1,187	1,882	4,877.00	3,203,246	2.59	656.84	50	594	2,476	6,412.84	4,212,209	32	1,008,801
1965	838	2,400	7,328.96	2,013,861	3.05	274.78	75	628	3,028	9,235.40	2,537,703	26	523,842
1966	781	2,086	4,256.82	1,403,623	2.04	329.74	75	586	2,672	5,450.88	1,797,373	28	393,750
1967	736	2,010	3,646.80	1,263,116	1.81	346.36	75	552	2,562	4,637.22	1,688,876	27	425,760
1968	1,055	2,177	4,227.41	1,539,617	1.94	364.20	75	791	2,967	5,755.98	2,096,328	36	556,711
1969	864	1,743	2,704.94	1,245,204	1.55	460.34	75	648	2,391	3,706.05	1,706,043	37	460,839
1970	1,017	1,894	3,334.46	1,496,919	1.76	448.92	75	763	2,657	4,676.32	2,099,294	40	602,375
1971	1,334	2,013	6,051.39	2,752,710	3.01	454.89	75	1,000	3,013	9,069.13	4,125,456	50	1,372,746
1972	1,187	1,882	4,952.12	2,949,372	2.63	595.58	75	890	2,772	7,290.36	4,341,993	47	1,392,621
1973	1,187	1,882	4,877.00	3,203,246	2.59	656.84	75	890	2,772	7,179.48	4,715,770	47	1,512,361
1965	838	2,400	7,328.96	2,013,861	3.05	274.78	100	838	3,238	9,875.90	2,713,700	35	699,839
1966	781	2,086	4,256.82	1,403,623	2.04	329.74	100	781	2,867	5,848.68	1,928,544	37	524,921
1967	736	2,010	3,646.80	1,263,116	1.81	346.36	100	736	2,746	4,970.26	1,721,499	36	458,383
1968	1.055	2,177	4,227.41	1,539,617	1.94	364.20	100	1,055	3,232	6,270.08	2,283,563	48	743,946
1969	864	1,743	2,704.94	1,245,204	1.55	460.34	100	864	2,607	4,040.85	1,860,165	49	614,961
1970	1,017	1,894	3,334.46	1,496,919	1.76	448.92	100	1,017	2,911	5,123.36	2,299,979	54	803,060
1971	1,334	2,013	6,051.39	2,752,710	3.01	454.89	100	1,334	3,347	10,074.47	4,582,776	66	1,830,066
1972	1,187	1,882	4,952.12	2,949,372	2.63	595.58	100	1,187	3,069	8,071.47	4,807,206	63	1,857,834
1973	1,187	1,882	4,877.00	3,203,246	2.59	656.84	100	1,187	3,069	7,948.71	5,221,031	64	2,041,268

Table 2.—Catch, baiting effort, and catch per effort in the fishery for nehu in Hawaiian waters, 1965-72. Percentages of the catch and the effort expended, by day and night baiting operations, are given in parentheses. (Note: The total catch from both day- and night-baiting operations for each year is not the same as that shown in Table 1 because some catch reports failed to designate when the catches were made.) (U.S. NMFS, 1973, see text footnote 2.)

Year	Catch		Baiting effort		Catch per effort	
	Day	Night	Day	Night	Day	Night
	Buckets	*Buckets*			*Buckets*	*Buckets*
1965	19,972 (58)	14,251 (42)	838 (37)	1,424 (63)	23.8	10.0
1966	20,696 (67)	10,242 (33)	781 (44)	1,011 (56)	26.5	10.1
1967	22,336 (71)	9,187 (29)	736 (45)	913 (55)	30.4	10.1
1968	30,148 (86)	4,911 (14)	1,055 (66)	544 (34)	28.6	9.0
1969	25,535 (86)	4,164 (14)	864 (70)	374 (30)	29.6	11.1
1970	30,332 (92)	2,724 (8)	1,017 (78)	290 (22)	29.8	9.4
1971	38,786 (93)	2,776 (7)	1,334 (82)	288 (18)	29.1	9.6
1972	36,713 (94)	2,187 (6)	1,187 (85)	206 (15)	30.9	10.6

Average for 1971 and 1972 = 37,748 + 2,482 = 40,230 buckets = B

$$Q_b = \frac{(4{,}877\text{ tons of tuna caught 1973})\,(2{,}204.6\text{ lb/t})}{40{,}230\text{ buckets}}$$

$$= \frac{10{,}751{,}129\text{ lb}}{40{,}230} = 267\text{ lb of tuna/bucket of bait.}$$

This is the price that the fisherman indirectly pays per bucket of baitfish caught. If a baitfish could be offered at a price less than this, the fisherman should, in principle, be willing to buy it since it would be more economical to do so than to catch his own.

COST ESTIMATE FOR CONSTRUCTION OF A COMMERCIAL TILAPIA PRODUCTION PLANT

HBS was run by the State Division of Fish and Game. Construction was finished in March 1962 and rearing of tilapia commenced immediately thereafter. Termination of this pilot project occurred in July 1965 because of the lack of demand by the commercial fisherman in spite of a plentiful supply of skipjack tuna that year.

The total construction costs (1962 prices) for the 10 brood tank, 44 fry-holding tank facility, and a small residence are shown below.

CONSTRUCTION

A. Contract work items		$119,070.00
B. Design engineering		
1. Field survey	—	
2. Subsurface inspection	—	
3. Office engineering	$8,248.08	
4. Consultant services	350.00	
5. Blueprinting	263.17	
6. Miscellaneous	132.70	
Subtotal		8,993.95
C. Construction engineering		
1. Field survey	—	
2. Material	113.44	
3. Office engineering	—	
4. Inspection	1,607.09	
5. Miscellaneous	5.98	
Subtotal		1,726.51
Total construction costs		$129,790.46

(Source: State Division of Fish and Game.)

As noted in the above figures, there were several areas which were completed at no cost to HBS, but which would have to be taken into account in the construction of such a plant by a private firm or individual. Consequently, a rounded figure of $130,000 is probably somewhat low.

HBS found after some time that this plant should have had an additional 16 fry tanks to handle the fry properly. This would have made a total of 10 brood tanks and 60 fry tanks. Assuming no difference between the cost of a brood and a fry tank, this would have increased construction costs by 23%. Since the $130,000 figure includes the residence, I used section A as the construction cost of the tanks, rounding this figure to $120,000.

$$\frac{(10 + 44)\text{ tanks}}{(10 + 60)\text{ tanks}} = 0.77\text{ or }77\%\text{ of the ideal facility actually constructed}$$

$$(\$120{,}000)/\,77\% = \$155{,}844\text{ would have been the cost of the ideal facility.}$$

Consequently, the construction cost for the complete 10 brood and 60 fry tank facility would have been approximately $166,000.

The increase in construction costs between 1962 and January 1974 was 64.4%.

$$(164.4\%)\ (\$166{,}000) = \$272.904.$$

The figure, therefore, for such a facility built as of 1 January 1974, would be approximately $273,000.

A commercial tilapia production plant requires about 2 acres of land. At $3.00/sq ft, this would cost $261,360, and land cost plus construction cost would total $534,360 (Tables 3, 4).

Table 3.—Total annual expense incurred raising tilapia on chicken feed; cost per bucket of bait-sized tilapia.

Total production and operating expenses (chicken feed)	$46,585.00	
Total construction and land costs (@ $3.00/sq ft) (2 acres)		$534,360.00
Total + 10% interest on construction and land costs (payable in 12 yr)	49,047.00	588,566.00
Annual total	$95,632.00	
Total fry production in pounds	51,082	
Cost per pound of bait (no profit)	1.87	
Cost per bucket (@ 7 lb/bucket)	13.09	
Cost per bucket (@ 10% profit)	14.40	
Cost per bucket (@ 20% profit)	15.71	

Table 4.—Total annual expense incurred raising tilapia on trout feed; cost per bucket of bait-sized tilapia.

Total production and operating expenses (trout feed)	$57,585.00	
Total construction and land costs (@ $3.00/sq ft) (2 acres)		$534,360.00
Total + 10% interest on construction and land costs (payable in 12 yr)	49,047.00	588,566.0(
Annual total	$106,632.00	
Total fry production in pounds	51,082	
Cost per pound of bait (no profit)	2.09	
Cost per bucket (@ 7 lb/bucket)	14.63	
Cost per bucket (@ 10% profit)	16.09	
Cost per bucket (@ 20% profit)	17.56	

OPERATING EXPENSES

Utility Costs

Electricity.—HBS paid an average of $375 per month for power. This would cover only 77% of the electricity costs of a 70-tank facility.

$$(\$375)/77\% = \$487.01.$$

The cost per kilowatt hour in 1962 was $0.03125.

$$\frac{\$487.01}{\$0.03125} \simeq 15{,}600 \text{ kwh/month.}$$

The cost per kilowatt hour for 1 January 1974 was $0.03351.

$$(\$0.03351)\ (15{,}600 \text{ kwh}) \simeq \$523.00.$$

Water.—The maximum rate of water usage at HBS was 40 gal/min (Table 5). Again (40 gal/min)/77% = 51.94 gal/min for the ideal case. This volume of water requires a code 06 m, with a monthly base charge at January 1974 rates of $7.50 (Board of Water Supply, Water Service Rate Schedule, effective 23 December 1970).

The average number of gallons of freshwater used per month would be 1,112,879 gal (Table 5) with the 23% increase included or 2,225,758 gal bimonthly. Bimonthly rates apply with a code 06 m.

Table 5.—Quantity of water used during one year of raising tilapia at Honolulu Bait Station.

Month	Gallons of fresh water
January	84,000
February	21,000
March	105,000
April	735,000
May	1,344,000
June	1,743,000
July	1,491,000
August	812,000
September	1,407,000
October	1,218,000
November	987,000
December	336,000
Total	10,283,000

$$\frac{10{,}283{,}000}{(12)\ (77\%)} = 1{,}112{,}879 \text{ gal/mo}$$

Using the maximum amount of water used in June, we can calculate the number of gallons per day and hour and minute:

$$\frac{1{,}743 \text{ gal/mo}}{30 \text{ days}} = 58{,}100 \text{ gal/day}$$

$$\frac{58{,}100 \text{ gal/day}}{24 \text{ h/day}} = 2{,}400 \text{ gal/h}$$

$$\frac{2{,}400 \text{ gal/h}}{60 \text{ min/h}} = 40 \text{ gal/min.}$$

First 100,000 gal @ $0.37/1,000 gal = $ 37.00
Next 700,000 gal @ $0.30/1,000 gal = 210.00
Next 2,000,000 gal @ $0.22/1,000 gal for 1,425,758 gal ≃ 314.00
Total bimonthly water costs $560.00

Sewer charges.—Although there are no sewer charges at this time, I feel that they should be included since they will probably have to be taken into consideration for any future plant operation. Proposed charges are substantial: $0.40/1,000 gal of freshwater used. For 1,112,879 gal/mo (Table 6), the cost would be approximately $445/mo.

Table 6.—Monthly and annual total operating expenses of tilapia rearing facility.

Operating expenses	Monthly	Annual
Utility costs:		
Electricity	$ 523.00	$ 6,276.00
Water	287.50	3,450.00
Sewer charges	445.00	5,340.00
Labor	2,125.00	25,500.00
Maintenance	68.25	819.00
Miscellaneous	100.00	1,200.00
Total	$3,548.75	$42,585.00

Labor

A facility such as this would require at least three persons for maintenance and operation. They would have the responsibilities of cleaning the tanks, handling the paper work, feeding the tilapia, and supervising the loading of the bait aboard fishing vessels. The annual wages of two employees with a GS-2 level and a supervisor with a GS-7 level would give a fairly accurate salary assessment. Current salaries run:

2 GS-2 @ $6,800 = $13,600 annually
1 GS-7 = 11,900 annually
Total $25,500 annually

Maintenance and Repair

Cost of maintenance and repair should run approximately 6% of the total construction cost of $273,000. Prorated over a 20-yr period, this equals $819/yr.

Miscellaneous Expenses

Approximately $1,200 a year should cover such items as office supplies and equipment. See Table 6 for total operating expenses.

PRODUCTION AND PRODUCTION COSTS

Brackish water breeding at HBS resulted in a threefold increase over that of the freshwater control. HBS estimates (the numbers were not as carefully controlled as the Hida et al. project) agreed closely with the Hida et al. (1962) report. The production at Paia, Maui, was 1,033 bait-size fish per female per year (Hida et al. 1962). Production with brackish water would have been 3 × 1,033 = 3,099 fry. With 3,000 females, the estimated annual production at HBS would have been 3,000 × 3,099 = 9,297,000 bait-size fish. With 182 bait-size fish equal to 1 lb (Brock and Takata 1955), the production for such a facility would be:

$$\frac{9{,}297{,}000}{182} = 51{,}082 \text{ lb of baitfish per year}$$

and

$$\frac{51{,}082 \text{ lb}}{7 \text{ lb/bucket}} = 7{,}297 \text{ buckets/yr.}$$

Feed requirements would run about 50,000 lb/yr. Chicken feed is currently about $0.08/lb and trout feed is approximately $0.30/lb. This gives:

Chicken feed = $4,000 annually or $334/mo
Trout feed = $15,000 annually or $1,250/mo.

The above data are given in Tables 3 and 4 and show the cost per bucket at 10% and 20% profits with these two types of feed. Since three persons could also operate a 20/120 plant, the cost per bucket should remain the same even after doubling this 70-tank facility. The price may even decrease. Depending upon the finances of the individual or firm, then, the size of the tilapia plant could theoretically be expanded to fill the entire fleet's live-bait needs, though I presently regard tilapia as only a supplemental baitfish.

Using the figures from Table 2 to obtain the number of buckets of bait caught, and my calculations of tilapia production, it is seen that this 10/60 commercial plant would provide 19% of the total day baitfish requirement for the present skipjack tuna fleet. If this plant were increased in size and production to, say, 25% of the total bait needs of the fleet, the projected value of its production can be seen in Table 1.

Effectiveness of Tilapia as Baitfish

I have so far assumed that tilapia would be as acceptable to the skipjack tuna fisherman as the currently used live bait, nehu. There are several points overlooked by such an assumption. First, the number of pounds of skipjack tuna caught per pound of bait used might differ between tilapia and nehu. Secondly, tilapia exhibit different swimming characteristics from nehu. Thirdly, the hooks currently used are shiny and somewhat similar in appearance to nehu; tilapia are darker in coloration and present a greater contrast to the hooks than do nehu.

The total mortality of nehu in the baitwells of the Hawaiian skipjack tuna fleet has been calculated by Yoshida et al. (1977) and found to average 21.7% from 1960 through 1972. For the period from 1954 through 1972 (Table 7), I obtained a mean value of 50.25 lb of tuna caught per pound of nehu used (see Calculations, p. 145). Nehu may be more efficient than this during the peak fishing season (May-September) and less so during the other months.

For comparison, I took information from all the literature which mentioned use of tilapia as skipjack tuna bait (Table 8). I converted the number of skipjack tuna taken with tilapia into pounds, using 18 lb as the average weight for tuna caught between May and September (King and Wilson 1957). From Shomura's (1964)

Table 7.—Annual catches of skipjack tuna and live bait from 1954 through 1972.

Year	Metric tons of skipjack	Buckets of nehu
1954	6,360.13	43,737
1955	4,397.43	49,712
1956	5,049.58	40,864
1957	2,780.66	30,638
1958	3,100.15	33,303
1959	5,630.65	37,637
1960	3,338.46	22,849
1961	4,941.66	37,092
1962	4,270.81	34,256
1963	3,673.86	32,670
1964	4,093.10	30,606
1965	7,328.96	36,352
1966	4,256.82	31,603
1967	3,646.80	31,832
1968	4,227.41	35,535
1969	2,704.94	30,096
1970	3,334.46	33,596
1971	6,051.39	42,098
1972	4,952.12	38,970
Total	84,139.39	675,446

Table 8.—Summary of number of tests conducted with tilapia as a live bait for pole-and-line fishing for skipjack tuna.

Date	Vessel	No. schools chummed w/tilapia	Scheme employed	No. buckets nehu	No. skip- jack[1]	Pounds skipjack caught	No. skipjack per bucket nehu	Pounds skipjack per pound nehu	No. buckets tilapia	No. skipjack per bucket tilapia	Pounds skipjack per pound tilapia
6/15/54	*Makua*	1	Attract with nehu, then chum with tilapia and nehu alternately.[2]	—	11 (small)	—	—	—	5	—	2.5 (assume 2 lb)
8/ 4/54	*Darling Dot*	2	Attract with nehu, then chum with nehu and tilapia.[2]	20	[3]313	8,184	—	—	2	—	104
9/21/54	*Buccaneer*	1	Attract with nehu, then chum with nehu initially then with tilapia alone.[2]	30	—	3,860	—	—	2	—	—
6/21/56	*Orion*	3	One school of three chummed first with tilapia. Nehu and tilapia may have been used in some.[4]	30	911/59	—	30.2	—	5	11.8	30.4
6/26/56	*Orion*	3	All three schools chummed first with tilapia.[4]	30	627/275	—	31.4	—	12	22.9	[5]59
7/11/56	*C. H. Gilbert*	6	Five schools chummed first with tilapia, others with nehu.[4]	—	56/—	—	3.5	—	—	—	—
7/12/56	*C. H. Gilbert*	2	Both schools chummed with tilapia only.[4]	2	—	—	—	—	2	—	—
7/26/56	*Marlin*	2	One school chummed first with tilapia, others with nehu.[4]	14	86/31	—	6.1	—	4	7.8	[5]20
7/27/56	*Marlin*	1	Chummed first with nehu, then tilapia.[4]	10	72/93	—	7.2	—	5	18.6	[5]48
8/10/56	*Buccaneer*	4	All four schools chummed first with tilapia, two others chummed first with nehu.[4]	5	12/1	—	2.4	—	4	0.1	—
9/22/56	*Buccaneer*	2	Both schools chummed only with tilapia.[4]	—	—	—	—	—	2	—	—
7/22/58	*Amberjack*	—	Tilapia and nehu used at discretion of fishermen. Estimate of buckets used derived from pounds used.[6]	17	—	4,110	26.6	30.7	5	14.0	16.2
8/25/58	*Olympic*	—	Same as above	14	—	9,000	21.7	68.8	6.5	15.4	48.6
8/30/58	*Olympic*	—	Same as above	—	—	4,500	—	—	6	21.0	53
9/ 4/58	*Olympic*	—	Same as above	6.4	—	9,000	22.4	44.4	4.6	40	79.2
7/ 8/59	*Tradewind*	—	Same as above	5	—	6,708	11.6	198.0	< 1	2.1	4.8
7/10/59	*Tradewind*	—	Same as above	26	—	9,100	21.7	35	2.6	2.1	5.0
7/10/59	*Sooty Tern*	—	Same as above	39.5	—	18,030	30	65	1.7	1.4	2.5
7/30/59	*Sailfish*	—	Same as above	12.8	—	5,600	31.7	56.7	2.6	10.5	27.5
7/31/59	*Sailfish*	—	Same as above	20.6	—	6,943	1.7	40.9	11.6	7.0	13.0
8/10/59	*Buccaneer*	—	Same as above	9	—	4,429	9.8	37.0	2	42.7	156.2
8/11/59	*Buccaneer*	—	Same as above	34	—	10,114	131.3	32.5	3	44.0	105.3
8/12/59	*Buccaneer*	—	Same as above	3	—	5,120	17.5	39.8	9	29.4	67.0
8/27/59	*Sailfish*	—	Same as above	13	—	15,000	—	55.5	15.4	—	92.5
9/ 5/59	*Sailfish*	—	Same as above	—	—	5,600	—	—	13	21.7	62.2
9/ 7/59	*Olympic*	—	Same as above	—	—	9,500	—	—	13	16.1	50.0
1952-62	*C. H. Gilbert*	6	Nehu and tilapia altered every 2 min.[7]	—	—	—	—	—	—	—	—
5/62-8/62	*Broadbill*	73	Used as live bait for pole-and-line fishing in connection with monofilament gill netting. Tests not designed to test tilapia as skipjack bait.[8]	—	—	—	—	—	—	—	57

[1] Number of skipjack tuna caught with nehu/number of skipjack tuna caught with tilapia.

[2] Source of data—Brock and Takata 1955.

[3] At approximately 19 lb per tuna.

[4] Source of data—King and Wilson 1957.

[5] Assume 18 lb per skipjack tuna due to time of year.

[6] Source of data—Hida et al. 1962.

[7] Source of data—Yuen 1969.

[8] Source of data—Shomura 1964.

data, I obtained a value of 57 lb of tuna per pound of bait. The average for the five papers consulted was 53 lb of skipjack tuna caught per pound of tilapia used. This agrees with Hida et al. (1962) at least in part because the large quantity of data that they contributed caused this final figure to be skewed in their direction.

I feel that this 53-lb figure may not be real, because, as can be seen in Table 8, the ratio between the amount of nehu used and the amount of tilapia used in these trials was quite high, and it appears that most, if not all, of the trials did not provide a nonbiased test for tilapia. The tilapia were probably used as if they were nehu, with little regard for tilapia's own special characteristics and associated problems, which also probably biases the data; but, observing the trial dates, it can be seen that they were conducted during the "fishing season," which could be the reason for a high efficiency figure. Evaluation of these different factors is difficult and will not be attempted here. However, it appears that the efficiency of tilapia, as measured by available data, is quite comparable to the efficiency of nehu in catching skipjack tuna.

As mentioned earlier, there are several problems with tilapia. They are slower swimmers than nehu, and with present fishing methods, the tilapia are "left behind," causing the tuna to fall behind also, and out of range of the pole and line. Tilapia reportedly have a tendency to sound, which also draws the tuna out of range of the pole and line.

The color contrast between nehu and tilapia makes the tilapia a less desirable supplemental baitfish, because the shiny hooks presently used more closely approach the coloration of nehu than that of tilapia. Thus the tuna might be able to differentiate more easily between the hooks and tilapia, making it less effective under the present fishing method.

Another drawback mentioned previously is the sharp dorsal spines that tilapia have, which are apt to injure the chummer's hands. For the size of a baitfish (3.8-6.4 cm), however, the spines should be too poorly developed to present a problem.

Problems and Advantages of Tilapia Culture

One major problem in culturing tilapia is the need for controlled growth. There is a need to cultivate the correct bait-sized fish, and predict when they will reach such a size. In addition, cannibalism occurs in this species, calling for a continuing separating procedure.

On the other hand, there are numerous advantages to using tilapia. They are very hardy and relatively easy to cultivate. They can be raised in fresh, brackish, or salt water, with proper acclimatization. Properly acclimatized, the mortality is negligible, say 5% at most, when held in a baitwell for extended periods. In addition, the fisherman probably will not have to "rest" the bait as he currently does.

Tilapia are edible, and fish that have grown beyond bait size could be sold for human consumption. A public information program would probably have to be carried out, however, before tilapia is readily accepted as food fish.

"Ogo," *Gracilaria coronopifolia*, an algae which is sold locally, could possibly be grown in conjunction with tilapia (E. L. Nakamura, Southeast Region, National Marine Fisheries Service, NOAA, Panama City, Fla., pers. commun.). Since it appears that tilapia do not actively feed upon this algae, it could be harvested, providing additional income and thus helping to defray the operating expenses of a tilapia production plant. There may be other species that could share the tilapia tanks and help defray operating costs while not harming, or being harmed by, the tilapia.

Enclosing the tanks and regulating the temperature could aid in maintaining a constant production throughout the year, and would provide protection from predators and poachers.

Fish Diseases, Cures, and Prevention

Knowledge of fish diseases or parasitic infestations is very important because they can kill a large quantity of fish in a matter of hours or a few days. Hatchery operators must constantly check the fish tanks and fish to ensure early detection and must institute treatment promptly.

Hida et al. (1962) described their problems. Their tanks remained almost disease free in 1958; a minor outbreak of the protozoan *Trichodina* occurred which was controlled by treatment with 0.5 ppm copper sulfate or 3 ppm potassium permanganate solution. They also encountered acute catarrhal enteritis, and because there was no known cure, they simply increased the flow of freshwater. They gave a prophylactic treatment of 3 ppm potassium permanganate or 0.5 ppm copper sulfate before adding new fry in 1959. They attributed their low infection rate, in part, to having an independent water supply for each tank instead of using recirculated water.

Uchida and King (1962) encountered infestations by the ectoparasite, *Trichodina*, and reported that potassium permanganate (3 ppm) was easiest to use and as effective as other methods. They used the same solution to control the protozoan *Chilodon*. Acute catarrhal enteritis, now called infectious pancreatic necrosis, is a viral infection which has characteristics similar to those caused by the protozoan *Octomitus salmonis*. The symptoms are whirling or corkscrewing accompanied by rapid ventilating, and subsequent sinking to the bottom and cessation of feeding. A "pin head" appearance results from this last symptom. Uchida and King found that by treating the feed with PMA (pyridylmercuric acetate) both of these latter diseases were eventually controlled. They also periodically added potassium permanganate as a prophylactic treatment. Their conclusion was that the single most important factor favoring diseases was overcrowding.

The HBS also encountered fish diseases. They had problems with a "whirling" disease and corrected this by changing the diet from pelleted dry feed to algae. Their prebait-size fish suffered from "pin head" a condition that was corrected by using filamentous algae collected from the ocean, alfalfa pellets, and cooked taro peels. This ailment was believed to have been caused by insufficient algae production in the tanks. They experienced heavy mortality among bait- and prebait-size fish caused by an unidentified disease. They treated this with a 12-h 0.8 ppm copper sulfate solution once every fourth day and increased the rate of water turnover from once every 2.5 days to once every 5 h.

FEATURES OF TANK CONSTRUCTION

The construction of the brood and fry tanks is very important in facilitating the overall operation of a tilapia plant. The cannibalistic characteristics of tilapia make it necessary to separate fry from the brood stock and different size fry from one another.

The HBS constructed a lip around the rim of the brood tanks that provided an area of refuge for the fry (Fig. 1). Periodically, this trough was emptied into fry tanks that had been "aged" with heavy growths of algae upon which the fry fed. There needs to be sufficient difference between the level of the trough and that of the fry tank to create a good head of water for flushing the fry easily and quickly from one location to another. There should also be a cascade arrangement between fry tanks for further separation after the fry begin to grow. Frames with different mesh sizes might also be used to separate the fry.

The bottom of the tanks should slope so as to drain properly and facilitate cleaning. Hose connections should be handy, and might even be saltwater outlets to reduce freshwater consumption.

Plumbing should be arranged so that water can be filtered and recirculated if desired, and proper lighting should be considered for night work and transferring the bait to the baitwells of the vessels.

A good pier with easy access both from land and sea should be available. Work saving devices might include a trough system to deliver bait to the baitwells, a movable crane, preferably motorized, for moving heavy objects, and an automatic feeder. The resulting ease of maintenance and operation would reduce personnel needs, helping to keep costs down.

CONCLUSIONS

In this paper I have analyzed the current break-even cost to the skipjack tuna fisherman of his bait, using an indirect method. I concluded that this cost, to the fisherman, is $30.12 per bucket of bait.

I analyzed the pilot tilapia production plant that was funded and run by the State Division of Fish and Game. From their raw data I drew a current cost estimate for a similar plant that could be theoretically increased to any size to handle either a portion or all of the bait needs of the current skipjack tuna fleet. Using the highest cost estimates, 10% interest on construction costs, land costing $3.00/sq ft payable over a 12-yr period, and using trout feed, I still obtained a cost per bucket of tilapia of $17.56. This includes a 20% profit for the producer.

Therefore I submit that if fishermen no longer catch bait, but purchase it instead and spend full time fishing, their bait will cost them less.

I also looked at the catch rates for tuna when using nehu and tilapia as bait, and found them to be comparable. Tilapia still need extensive trials as a bait species, however, and tilapia data need further scrutiny.

Tilapia characteristics, both favorable and unfavorable, were discussed and should offer some insight into the problems and advantages of raising tilapia. I also mentioned the possibility of sharing the tilapia tanks with a compatible, marketable species, and thereby helping to defray expenses.

Fish diseases contracted during three different baitfish rearing studies were reviewed, along with their treatments.

CALCULATIONS

$$C_0 = \frac{D_b}{D_f} V - (D_b \cdot C_d)$$

$$= \frac{1187}{1882} (\$3{,}203.246) - (1{,}187 \text{ days}) (\$38.46)$$

$$= \$1{,}974{,}674 \text{ net opportunity cost}$$

$$B_a = \frac{Q_a}{Q_b} = Q_a \frac{B_0}{Q_t}$$

= 3,072 tons (40,230 buckets/yr) / (4,877 tons caught for 1973)

= 25,341 buckets (additional amount of bait required to catch additional skipjack tuna)

$$B_t = (B_0 + B_a)$$

= (40,230 buckets) + (25,341 buckets)

= 65,571 buckets.

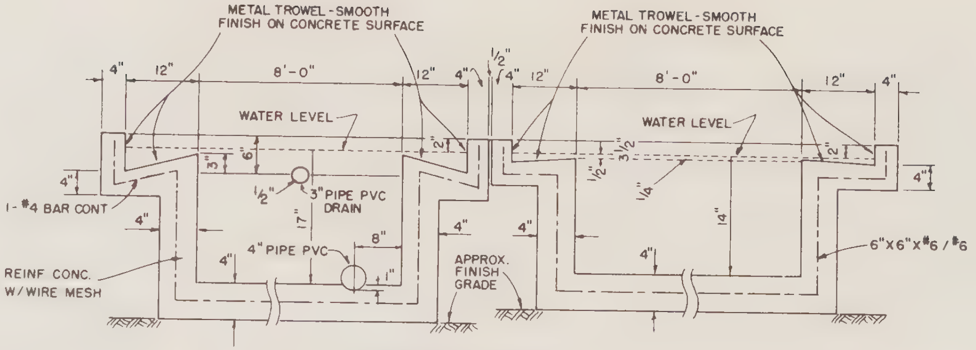
Break-even (maximum) price for nehu:

C_0/B_t = 1,974,674/65,571 = $30.12.

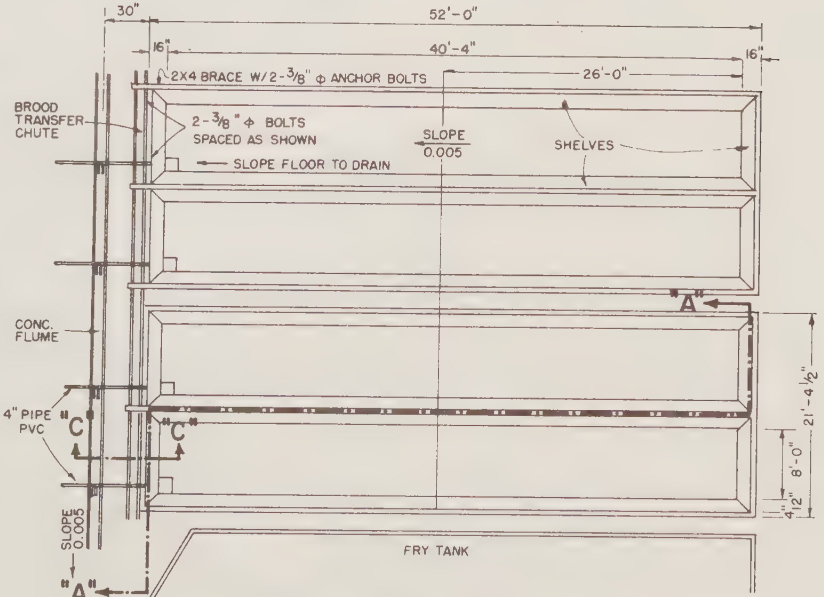
Determination of the number of pounds of tuna caught per pound of nehu used.

Total number of metric tons of skipjack tuna caught from 1954 through 1972 (from Table 7):

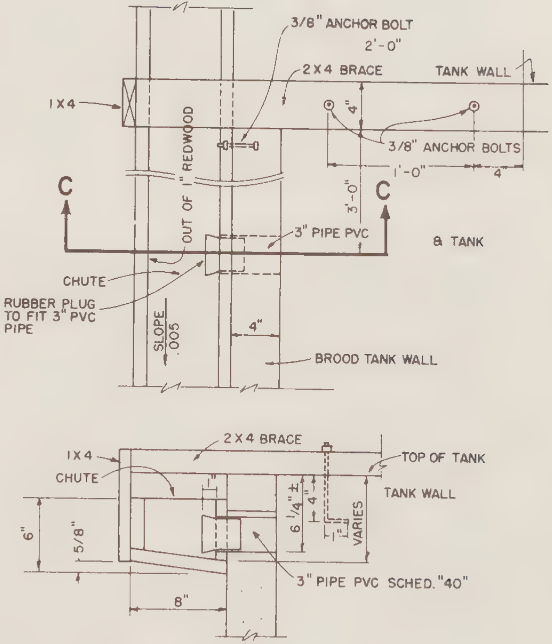
(84,139.39 t of tuna) (2,204.6 lb/t)
= 185,493,699 lb of tuna caught.
Total number of buckets of nehu caught, 1954-72: (673,446 buckets of nehu caught) (21.7% mortality)
= 146,137.782 buckets of nehu died


METAL TROWEL-SMOOTH FINISH ON CONCRETE SURFACE
METAL TROWEL-SMOOTH FINISH ON CONCRETE SURFACE
4"
12"
8'-0"
12"
4"
½"
4"
12"
8'-0"
12"
4"
WATER LEVEL
WATER LEVEL
2"
3"
6"
2"
3½"
½"
¼
2"
4"
4"
1-#4 BAR CONT
½"
3" PIPE PVC DRAIN
17"
14"
4"
4"
4"
4"
8"
4" PIPE PVC
1"
4"
4"
6"X6"X#6/#6
REINF CONC. W/WIRE MESH
APPROX. FINISH GRADE

SECTION "A-A"


30"
52'-0"
16"
40'-4"
16"
2X4 BRACE W/2-3/8" Φ ANCHOR BOLTS
26'-0"
BROOD TRANSFER CHUTE
2-3/8" Φ BOLTS SPACED AS SHOWN
SLOPE 0.005
SHELVES
SLOPE FLOOR TO DRAIN
"A"
CONC. FLUME
21'-4½"
4" PIPE PVC
"C"
"C"
8'-0"
12"
4"
SLOPE 0.005
"A"
FRY TANK

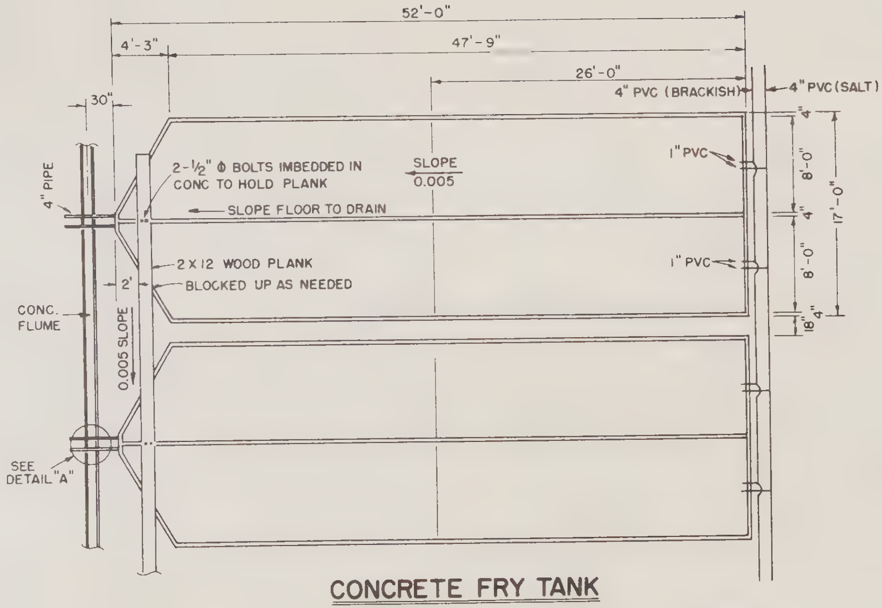
CONCRETE BROOD TANK


3/8" ANCHOR BOLT
2'-0"
2X4 BRACE
TANK WALL
1X4
4"
OUT OF 1" REDWOOD
3/8" ANCHOR BOLTS
1'-0"
4"
C
3'-0"
C
3" PIPE PVC
℄ TANK
CHUTE
RUBBER PLUG TO FIT 3" PVC PIPE
SLOPE .005
4"
BROOD TANK WALL
2X4 BRACE
1X4
TOP OF TANK
CHUTE
TANK WALL
1"
6¼"±
4"
1"
VARIES
6"
5/8"
3" PIPE PVC SCHED."40"
8"

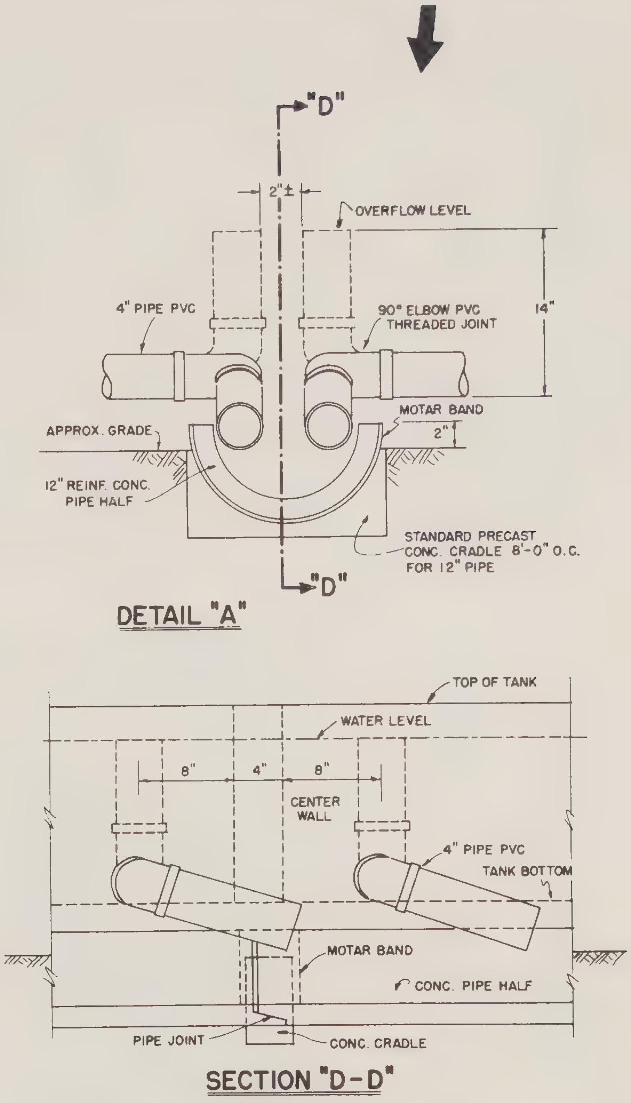
SECTION "C-C"
CHUTE DETAIL FOR BROOD TANK

Figure 1.—Copies of blueprints from which the Honolulu Bait Station constructed brood and fry tanks for the rearing of young tilapia.

A. Overall plan for the concrete brood tank.
B. Detailed end view of two concrete brood tanks.
C. Chute detail of brood tank.
D. Detail of concrete drain flume.
E. Concrete tank for rearing tilapia fry.


52'-0"
4'-3"
47'-9"
26'-0"
30"
4" PVC (BRACKISH)
4" PVC (SALT)
4"
8'-0"
4"
8'-0"
4"
18"
17'-0"
1" PVC
1" PVC
2-½" Φ BOLTS IMBEDDED IN CONC TO HOLD PLANK
SLOPE 0.005
SLOPE FLOOR TO DRAIN
2 X 12 WOOD PLANK
BLOCKED UP AS NEEDED
2'
0.005 SLOPE
4" PIPE
CONC. FLUME
SEE DETAIL "A"

CONCRETE FRY TANK


"D"
2"±
OVERFLOW LEVEL
4" PIPE PVC
90° ELBOW PVC THREADED JOINT
14"
MOTAR BAND
2"
APPROX. GRADE
12" REINF. CONC. PIPE HALF
STANDARD PRECAST CONC. CRADLE 8'-0" O.C. FOR 12" PIPE
"D"
TOP OF TANK
WATER LEVEL
8"
4"
8"
CENTER WALL
4" PIPE PVC
TANK BOTTOM
MOTAR BAND
CONC. PIPE HALF
PIPE JOINT
CONC. CRADLE

DETAIL "A"

SECTION "D-D"

(673,446) − (146,137) = 527,308 buckets of nehu used

$$\frac{\text{185,493,699 lb of tuna caught}}{\text{527,308 buckets of nehu used}} = \text{351.77 lb of tuna/bucket of nehu}$$

$$\frac{\text{351.77 lb of tuna/bucket of nehu}}{\text{7 lb. of nehu/bucket}} = \text{50.25 lb of tuna/lb of nehu used}$$

ACKNOWLEDGMENTS

I thank the Division of Fish and Game of the Department of Land and Natural Resources of the State of Hawaii for allowing me access to their files and the use of the raw data gathered at their Honolulu Bait Station during the years 1962 through 1965. Without their data this paper could never have been written. I extend my personal thanks to Michio Takata, Director of the State Fish and Game Division, for granting me permission to publish their data and to Takuji Fujimura, who had to bear with all my questioning and who supplied many of the ideas incorporated into this paper. I express my indebtedness to Richard N. Uchida, Thomas S. Hida, and Tamio Otsu at the Honolulu Laboratory, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, who took many of their busy hours to help me.

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EFFECT OF DISSOLVED OXYGEN CONCENTRATION AND SALINITY ON SWIMMING SPEED OF TWO SPECIES OF TUNAS

Studies on captive skipjack tuna, *Katsuwonus pelamis*, have determined three physiological parameters that may operate to delimit oceanic distribution of this fish. If 1) a lower temperature limit of 18°C, 2) a size-dependent upper temperature limit, and 3) a lower oxygen limit of 5 ppm are mapped onto the temperature and oxygen levels of the central Pacific area, the resulting model is consistent with many of the peculiar features of the geographical distribution of the skipjack tuna (Barkley et al.[1]). In particular, the exclusion of adult skipjack tuna from warm, oxygen-poor waters of the eastern tropical Pacific Ocean is explained.

But the physiological parameters used in the model were either speculative—upper temperature limits—or based upon acute and stressful experimental conditions—lower oxygen and temperature limits. Gooding and Neill[2] determined the lower oxygen limit by introducing tunas into a small tank (1.8 × 2.4 × 0.6 m oval) containing seawater at a given level of oxygen saturation. Swimming speed and survival time were measured. They found that survival time and swimming speed were independent of oxygen levels in excess of 4 ppm; below 4 ppm survival time was directly and swimming speed inversely proportional to dissolved oxygen amounts. So apparently 4 ppm is close to the incipient lower lethal limit for skipjack tuna under the given experimental conditions. For modeling distribution limits, Barkley et al. (see footnote 1) used a more conservative figure of 5 ppm.

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[1] Barkley, R. A., W. H. Neill, and R. M. Gooding. Skipjack tuna habitat based on temperature and oxygen requirements. Manusc. in prep. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812. (Material presented at 26th Tuna Conference, Lake Arrowhead, Calif., 29 Sept.–1 Oct. 1975.)

[2] Gooding, R. M., and W. H. Neill. Respiration rates and reactions to low oxygen concentrations in skipjack tuna, *Katsuwonus pelamis*. Manusc. in prep. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.

However, a physiological limit of 4 or 5 ppm is not necessarily a behavioral limit; if the limit is approached slowly under natural and otherwise unstressful conditions, can a fish adaptively respond? Whitmore et al. (1960) found that coho salmon, *Oncorhynchus kisutch*, avoided water of lowered oxygen levels yet which produced no respiratory distress. In contrast, kawakawa, *Euthynnus affinis*, a species closely related to skipjack tuna, tolerated 2-ppm water for short periods in order to get food (Chang and Dizon[3]).

In the present experiment, I tested the responses of free-swimming tunas—both skipjack tuna and yellowfin tuna, *Thunnus albacares*—encountering slowly changing oxygen levels. The rate of change was comparable with that which a tuna might encounter in nature. Yellowfin tuna were tested for comparison because they are abundant in the same areas of the eastern tropical Pacific avoided by large skipjack tuna. Finally, salinity fronts have been suggested as a factor determining distribution, so responses to decreasing salinity levels were also examined.

Materials and Methods

Eight skipjack tuna and three yellowfin tuna were tested with decreasing oxygen levels, and three skipjack tuna, and one yellowfin tuna were tested with decreasing salinity levels. Fish were chosen from stocks at the Kewalo Research Facility of the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, Hawaii. Tuna stocks for this experiment were kept in outdoor tanks (7.3 m diameter × 1.2 m deep) until used; they were then removed by angling with a barbless hook and transferred to the swim chamber in a plastic bag partially filled with water. This is a good transfer technique since fish on occasion have fed immediately after transfer.

The responses of tunas to decreasing oxygen and salinity levels were examined in a tank system consisting of a swim chamber equipped with photocells for monitoring and recording fish behavior. (For details see Dizon et al. 1977.) The swim chamber was a 6.1 m diameter × 0.61 m deep fiber glass tank fitted with a concentric inner wall so the fish was constrained to swim in a 0.75-m channel around the periphery. Six laps equaled 100 m. Water (24°C) was introduced and removed from the swim channel through two pairs of concentric rings of polyvinyl chloride pipe. Entering (or exiting) water divided equally into two inflow (or outflow) pipes, each flowing countercurrent to the other to provide minimum oxygen or salinity asymmetry and horizontal transport of water within the swim channel. Water was recirculated through an outside circuit at 1,136 liters/min to insure thorough mixing of any introduced new water. New seawater was added to the tank at 38 liters/min.

Oxygen was reduced in the tank by replacing the 38 liters/min new seawater with 38 liters/min anoxic seawater obtained at our well head before aeration and introduced into the intake of the 1,136 liters/min recirculation pump. Oxygen decreased approximately exponentially within the swim chamber—0.06 ppm/min after 30 min and 0.03 ppm/min after 60 min. Salinity levels in the swim chamber were reduced by introducing aerated freshwater (38 liters/min) into the pump intake. Salinity decreased exponentially—0.07‰/min after 30 min and 0.03‰/min after 60 min.

Passage of the fish was sensed at four photocell stations (six photocells/station) at 90° intervals around the periphery of the swim channel. Information from the photocells was translated into swimming speed (minutes per lap), direction (clockwise or counterclockwise), and frequency of reversals or swimming direction by digital logic equipment and printed on adding machine tape.

Procedures were quite simple; tuna (starved for 1 day) were moved into the tank and allowed 100 min to habituate; swimming speeds were continuously recorded to provide baseline data to compare with behavior during periods of changing oxygen or salinity. After 100 min, a test was started and behavior was recorded as salinity or oxygen decreased. Oxygen and salinity levels were allowed to reach 2 ppm and 29‰, respectively. After reaching these levels (about 200 min), test water was shut down and normal seawater restored. The following morning fish were removed, weighed, and measured, and survivors were returned to holding tanks. Oxygen and salinity levels were monitored by oxygen meter and salinograph; samples were taken periodically for laboratory analysis to verify the instruments.

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[3] Chang, R. K. C., and A. E. Dizon. Low oxygen levels as barriers to voluntary movements of tunas. Manusc. in prep. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812. (Material presented at 26th Tuna Conference, Lake Arrowhead, Calif., 29 Sept.-1 Oct. 1975.)

Results and Discussion

Behavioral responses to decreasing levels of salinity were unremarkable; Table 1 summarizes results from three skipjack tuna and one yellowfin tuna. No consistent swimming speed changes were observed during periods when salinity decreased from about 34‰ to 29‰. Although sample size is small, these tunas did not make any dramatic response to salinity changes of magnitudes expected within their normal habitat.

Figure 1 illustrates typical results from tunas encountering slowly changing oxygen concentration. At or about 4 ppm, skipjack tuna (Figure 1a) demonstrated an abrupt increase in swimming speed. In most fish tested, speed increased to over 2 lengths/s. Yellowfin tuna, in contrast, showed no alteration in swimming speed as oxygen levels decreased (Figure 1b).

Figure 2 summarizes the oxygen experiment observations from eight skipjack tuna and three yellowfin tuna. Individual points plotted are median swimming speeds for the eight skipjack tuna grouped by: 1) before treatment and 2) 1-ppm dissolved oxygen intervals both decreasing and increasing, i.e., 6–5, 5–4, 4–3, 3–2, and 2–3, 3–4, 4–5, 5–6. Number of swimming speeds sampled ranged from under 5 to over 100 depending on the number of laps swum during each interval. Heavy line connects the grand median of each interval. Similar data for each yellowfin tuna (decreasing oxygen intervals only) are included for comparison.

TABLE 1.—Effect of decreasing salinity on mean swimming speed in tunas.

Item	*n*	$\bar{X}$ (length s)	SD
Skipjack tuna 1 (38.3 cm, 925 g)			
Before salinity change	28	2.10	0.40
During salinity change	22	1.82	0.40
Skipjack tuna 2 (37.7 cm, 882 g)			
Before salinity change	44	2.03	0.26
During salinity change	12	2.37	0.19
Skipjack tuna 3 (42.0 cm, 1,352 g)			
Before salinity change	30	1.21	0.07
During salinity change	15	1.16	0.06
Yellowfin tuna 1 (45.3 cm, 1,491 g)			
Before salinity change	39	1.54	0.30
During salinity change	31	1.81	0.26

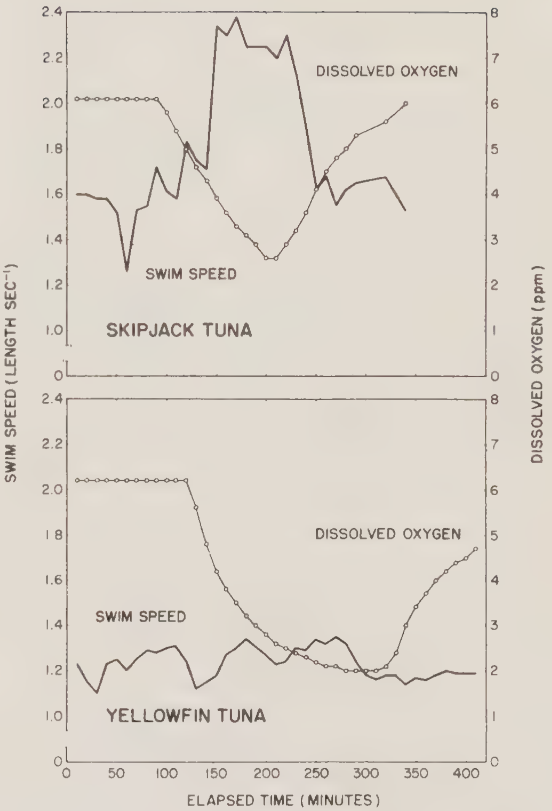

FIGURE 1.—Effect of dissolved oxygen level on swim speed in two species of tunas. Swim speeds are median values sampled for 10-min periods.

Not all of the skipjack tuna survived the treatment; three of the eight died when oxygen levels dropped below about 2.5 ppm. Survival times for skipjack tuna under conditions of low oxygen are as follows: in excess of 240 min at 4 ppm, 59 min at 3 ppm, and 18 min at 2 ppm (Gooding and Neill see footnote 2). My data are consistent with this resistance–time distribution, and both studies support the Barkley et al. (see footnote 1) hypothesis that there does exist a low oxygen level that limits the observed oceanic distribution of skipjack tuna.

Yellowfin tuna are not apparently stressed during the exposures to the low oxygen water employed. In separate tests done after the exposures to decreasing oxygen, two additional yellowfin tuna survived and made no overt locomotory changes when introduced directly into water

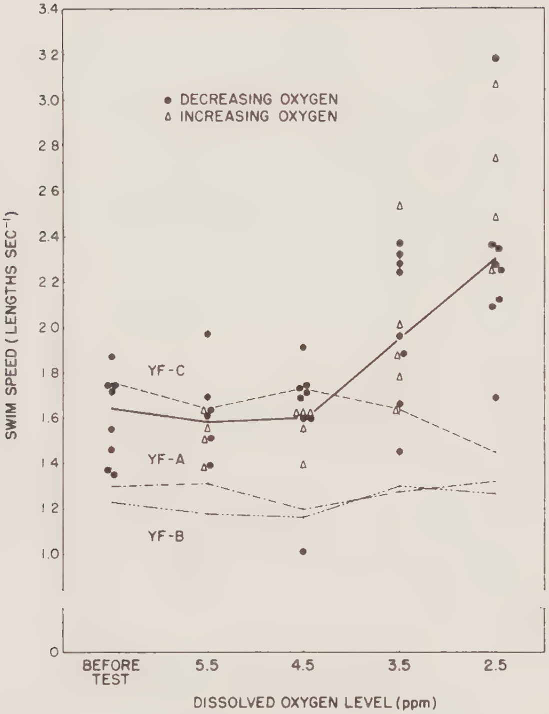

FIGURE 2.—Summary of data from the oxygen experiment observations from eight skipjack tuna and three yellowfin tuna. Dots — decreasing oxygen levels, median swim speeds grouped by 1-ppm intervals and "before" test observations. Open triangles — increasing oxygen levels, median swim speeds grouped by 1-ppm intervals. Solid line — grand median for eight skipjack tuna. Broken lines — medians for each of the three yellowfin tuna, decreasing oxygen levels only.

containing 1.4 and 1.6 ppm oxygen. They survived a 200-min exposure and a 100-min recovery period. By way of contrast, brook trout, *Salvelinus fontinalis*, LD_{50}'s for 1.5 ppm and 1.4 ppm were 300 and 100 min, respectively (Shepard 1955). The brook trout and the yellowfin tuna were swimming at about the same speeds, 1.0–1.5 lengths/s. Although conditions of the two experiments are in no way similar, these data do imply that yellowfin tuna are at least as low oxygen tolerant as brook trout. The higher energy requirements (larger fish, warmer water) of yellowfin tuna allow this conclusion. Perhaps if oxygen levels dropped low enough in my tank (1.4 ppm is about the lowest that could be achieved), an increase in speed similar to that in skipjack tuna would have been observed.

Increased swimming speed should function either to remove the fish from suboptimal areas (if coupled with some directive stimuli) or to provide more water to the gills—tunas are ram ventilators. Within the skipjack tuna habitat, water deficient in oxygen is found within and below the thermocline (Barkley et al. see footnote 1). Appropriate behavior would be to swim up and out of the low-oxygen water. Even without a change in direction, angle of attack of pectoral fins, or body attitude, increased swimming speed alone will cause a tuna to rise due to increased lift (Magnuson 1973).

Faster swimming speeds do not seem to be a response to increase ram ventilation (open mouth swimming). Increased flow over the gills providing more oxygen delivery is offset by increased respiratory demands imposed by faster swimming. Under conditions of saturated seawater (7.2 mg O_2/liter), 15% head loss along the respiratory flow path (Brown and Muir 1970), a conservative oxygen utilization factor of 75% (Stevens 1972), and a 1 cm^2 mouth gape (Brown and Muir 1970), oxygen is delivered to the gills at the rate represented by the middle broken line (Figure 3). This, of course, also increases as swimming speed increases. Respiratory demand (solid black line) and oxygen delivery intersect at two points: the lower is at the minimum swimming speed that can still furnish sufficient oxygen for an animal in an almost basal state and the upper is a point at which exponentially increasing respiratory demand again exceeds linearly increasing oxygen delivery.

The latter would seem to be maximum sustained swimming speed; anaerobic metabolism would be necessary at speeds above. However, neither function (anaerobic or aerobic) may be correctly extrapolated to the faster swimming speeds. Respiratory demand might well be less at higher speeds if swimming efficiency increases.

Yet, if dissolved oxygen concentration drops to 4 ppm, increase in swimming speed is an inefficient way to make up the deficit (lower broken line). But, increase gape to 2 cm^2 (I am assuming for argument's sake that this doubles ventilation volume) restores the amount of oxygen delivered (upper broken line). In summary, I suspect that increased swimming speed of skipjack tuna encountering oxygen-deficient water is not due to ram ventilation needs but rather is a behavioral response to remove an animal from a suboptimal area. Considering the relative expense of faster swimming in terms of oxygen needs, the modest increases in swimming speeds observed are probably very adaptive in that they should cause a

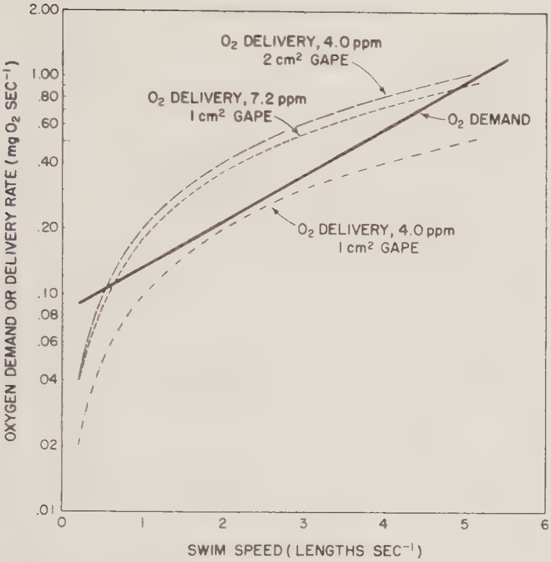

FIGURE 3.—Respiratory demand (Gooding and Neill see footnote 2) versus respiratory supply (Brown and Muir 1970; Stevens 1972) as a function of swimming speed in a 40-cm, 1.4-kg skipjack tuna. Respiratory demand increases geometrically while respiratory supply increases arithmetically with increasing swimming speed. When oxygen concentration decreases it is more efficient to increase ram ventilation by increasing gape rather than simply swimming faster.

fairly rapid rise in the water column at a relatively low energetic cost. Yellowfin tuna, in contrast, are just not stressed at the levels of saturation employed in our experiments. Yellowfin tuna should be able to occur in the anoxic water in or below the thermocline and since in the eastern central Pacific Ocean anoxic, cool waters are as inhospitable as the upper too warm waters, skipjack tuna may find no suitable habitat.

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7712

Env. Biol. Fish. Vol. 2, No. 1, pp. 83–92, 1977

RAPID TEMPERATURE COMPENSATION OF VOLITIONAL SWIMMING SPEEDS AND LETHAL TEMPERATURES IN TROPICAL TUNAS (SCOMBRIDAE)

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Keywords:
Thermoregulation, Tunas, Swimming speed, Temperature tolerance, Acclimation

Synopsis

Observations on continuously swimming tunas were used to determine effects of temperature upon volitional locomotory activity and to determine upper and lower lethal temperatures. Experimental subjects were 10 skipjack tuna, *Katsuwonus pelamis*, 9 kawakawa, *Euthynnus affinis*, and 3 yellowfin tuna, *Thunnus albacares*.

Our results: lower and upper lethal temperatures for the euthynnids (*K. pelamis* and *E. affinis*) were 15° and 33° C, respectively. Swimming speed for the euthynnids did not decrease with temperature within most of the zone of thermal tolerance; we observed either temperature independence or increases in speed as the temperature decreased. Yellowfin tuna swam slower as the water temperature decreased, but swimming speed changes lagged behind the water temperature changes. This effect was most certainly due to the large thermal inertia that is a property of tunas. The lag between swim speed and water temperature was eliminated by utilizing an estimate of red muscle temperature, rather than water temperature, as a covariate. Yellowfin tuna swim speed was best correlated with red muscle temperature rather than ambient water or brain temperatures.

Received 12.8.1976 Accepted 24.12.1976

Introduction

Most animals respond to temperature change with changed rates of respiration and activity. In general, Q_{10}'s range from 2 to 3 (Prosser & Brown 1961). Yet, for animals that live in heterothermal environments, processes that vary more than twofold for every 10° change should be disadvantageous. Homeotherms have circumvented the problem by controlling temperature of their tissues. Poikilotherms can avoid temperature fluctuations by behavioral thermoregulation, compensate for temperature changes at some level of integration (subcellular to behavioral) or tolerate thermally induced variations in metabolism and activity.

Within their zone of thermal tolerance, tunas apparently have the ability to compensate for rapid temperature fluctuations so that locomotory activity and routine metabolism are independent of temperature. Stevens & Fry (1972) observed that routine swimming speed of two skipjack tuna, *Katsuwonus pelamis*, was relatively constant during rapid temperature change of 10° C. Chang, Ito & Neill (MS)* demonstrated that activity and respiratory rate of skipjack tuna were the same at three temperatures (20°, 24°, and 28° C). Because fish were held 4 h at test temperatures before oxygen measurements were made, some acclimation was possible. Earlier, Gordon (1968) had found that in vitro metabolism of red and white tuna muscles was almost constant over a large temperature range (5°–35° C).

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* Chang, R. K. C., B. M. Ito & W. H. Neill. Temperature independence of metabolism and activity of skipjack tuna, *Katsuwonus pelamis*. Manuscript in preparation. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

In the present paper, we first report upper and lower lethal temperatures for skipjack tuna and kawakawa, *Euthynnus affinis*. For both these and a third species, yellowfin tuna, *Thunnus albacares*, we then present experiments that relate volitional swimming speed to the level and rate of change of environmental temperatures.

Lethal temperatures

Upper and lower lethal temperatures were estimated for skipjack tuna (30–36 cm FL (fork length)) and kawakawa (44–50 cm FL) by increasing or decreasing water temperature 1° C day^{-1}. Initially, water temperatures were about 24° C in three test tanks. One fish was transferred into each test tank from large holding tanks at a similar temperature at least three days before testing began. Then temperature was raised in one tank, lowered in another, and held constant in the third. Animals and treatments were allocated randomly to the tanks with the restriction that each run would have an increasing, a decreasing, and a constant temperature. A run was completed when death temperatures had been reached for the warmed and the cooled fish. Fish were offered thawed smelt daily, and the temperature at which they last took food was also recorded.

Test tanks were 0.6 m deep, 2.4 m in diameter, and were continuously replenished with 120 liters h^{-1} of new water. Sources of heat (quartz glass-sheathed immersion heaters) and cooling (epoxy-coated, stainless steel coils) were located in a vertical cylinder attached to and open at top and bottom to the test tank. The cylinder functioned as an air lift pump, pulling water from the bottom of the test tank, lifting it across the heating and cooling elements, and returning it to the tank at the surface. Mercury contact thermometers and relays controlled heaters and circulation of coolant.

The fish continued to eat some offered food until temperatures were within 1° and 2° C of lethal levels (Table 1). Lower tolerance limits were about 15° C and upper tolerance limits were 33° C. They were essentially the same for both species, and variations among individuals were small.

Swimming speed

Materials and methods

Fish were chosen from stocks maintained in large

Table 1. Lethal temperatures of skipjack tuna and kawakawa exposed to progressive temperature change of 1° C day^{-1}. Values are temperature at which they were alive and the last temperature at which they ate.

Species	Temperature (° C)			
	Lowest		Highest	
	Alive	Feeding	Feeding	Alive
Skipjack tuna	16	17	33	33
	16	17	34	34
	14	*15*	*33*	*33*
Medians	16	17	33	33
Kawakawa	15	16	33	34
	14	16	30	32
	15	–	–	*33*
Medians	15	16	31.5	33
Grand medians	15	16	33	33

Table 2. Outline of treatments during which locomotory activity was measured as a function of water temperature.

Species	Rate of temperature change					
	5° C h^{-1}			1° C day^{-1}		
	n	Fork length (cm)	Temperatures (° C)	n	Fork length (cm)	Temperatures (° C)
Skipjack tuna	4	45–47	27 → 18	3	30–36	24 → 34
				3	30–33	24 → 14
Kawakawa	3	41–45	29 → 18	3	40–50	24 → 34
				3	45–47	24 → 14
Yellowfin tuna	3	41–56	31 → 20			
	1	41	21 → 29			

tanks at the Kewalo Research Facility of the Southwest Fisheries Center, National Marine Fisheries Service, Honolulu, Hawaii. They were caught by angling with a barbless hook and then transferred in a plastic bag partially filled with seawater. On occasion, fish handled this way have fed immediately. After a test, fork length was measured.

Fish were tested with two rates of temperature change: a treatment comparable to Stevens & Fry (1972) in which temperature changed at 5° C h^{-1}, and a treatment in which temperature was changed much slower – 1° C day^{-1}. Table 2 summarizes treatments and subjects.

1° C per day

Data were collected in the course of the lethal-temperature experiment. Fish were placed in three tanks (described above), one of which served as a control. Swimming performance of the fish in treatment tanks (increasing temperature 1° C day^{-1} or decreasing temperature 1° C day^{-1}) was measured relative to the control. Activity was estimated once before dawn and again at midday prior to feeding them. The number of seconds elapsing during 10 tail beats was recorded at least three times at each observation. The median was converted to tail beats per minute, the control value was subtracted, and this difference was averaged for the two times of observation. The last result, tail beats per second for treatment minus control, gave a number to associate with water temperature. Thermostats were advanced at the end of each light period and tanks reached their new temperatures 8 to 10 h prior to the next observation period.

Attempts to use a 16 mm cine camera to measure swimming speed were successful only for skipjack tuna. Speeds were extracted through frame-by-frame analyses of films spaced throughout the light period prior to feeding time. Results were calculated in terms of body length per second, the simplest and most useful method of comparing swim speeds (Webb 1974).

5° C per hour

Tests were performed in a large ring-shaped tank in which a tuna swam laps that were timed with photocells to give swimming speed. The fiber glass tank had two concentric walls, one at 6 m diameter and the second at 4.5 m diameter. The resulting circular channel was 0.75 m wide and 0.5 m deep – six laps equalled 100 m. To cool the tank, water was removed from the channel, chilled in transit through a stainless steel heat exchanger, and pumped back at the rate of 19 liters sec^{-1} (1 volume every 4.5 h).

Passage of the fish was sensed at four photocell stations (six photocells per station) at 90° intervals around the periphery of the channel. Information from the photocells was translated into minutes per lap by digital logic equipment and printed every six laps.

Swimming speeds were measured for 100 min prior to lowering temperature. The temperature was then lowered to about 20° C, the chiller was shut down and tank temperature allowed to rise overnight.

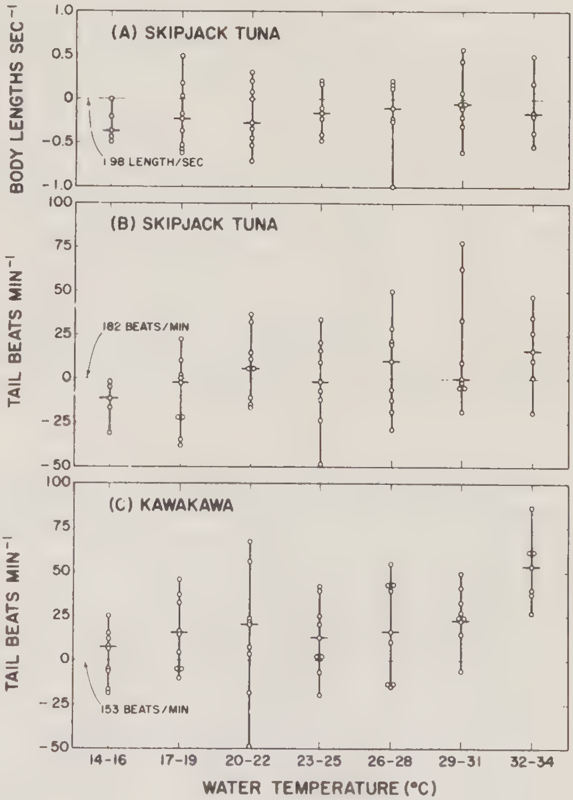

Fig. 1. Influence of temperature changing at 1° C day^{-1} from 24° C on the locomotory activity of skipjack tuna and kawakawa. Controls were held at 24° C; activities are plotted as differences from mean activities of controls. Short horizontal bars are grand medians of the experimental subjects.

Fish were subjected to two or three periods of declining temperatures on consecutive days. For one yellowfin tuna, temperature was kept low all night and data were collected during the recovery period the next morning.

Speed in minutes per lap was converted to body lengths per second. Red muscle and brain temperatures were estimated by the method of Neill & Stevens (1974) using parameters determined by Neill, Chang & Dizon (1976). Log_{10} speeds were regressed on either water temperature or red muscle temperature.

Results

1° C per day

For both skipjack tuna and kawakawa, swimming speed from lower to upper lethal temperatures appeared remarkably unrelated to water temperature changing at 1° C day^{-1} (Fig. 1). For skipjack tuna none of the differences for tail beats or swim speed were significant among temperatures grouped by 3° C (Kruskal-Wallis 1-way AOV). But differences in tail beat frequencies among temperature treatments for kawakawa were significant ($P \leq 0.05$, Kruskal-Wallis 1-way AOV). A multiple comparison test of the kawakawa data (Hollander & Wolfe 1973, p. 125) indicated that the only significant difference was between the two extreme temperature groups, i.e., tail beat rate at 14°–16°C was less than that at 32°–34°C.

Linear regressions of tail beat differences from control on temperature (not grouped by 3° C) were similar for skipjack tuna and kawakawa. Standard errors of the estimate were reduced by using a log transformation of the tail beats per minute difference from control. The regression model thus obtained was $\log_{10}(A + 100) = 1.84327 + 0.006687T + \text{error}$ ($n = 57$, $r = 0.36$, $P \leq 0.05$) for skipjack tuna and $\log_{10}(A + 100) = 1.89401 + 0.007137T + \text{error}$ ($n = 61$, $r = 0.43$, $P \leq 0.01$) for kawakawa. A is tail beats per minute difference from control and T is Celsius degrees. For control fish, tail beats per minute were 182 min^{-1} for skipjack tuna and 153 min^{-1} for kawakawa. Thus, at a rate of change of 1° C day^{-1}, the volitional swimming activities of skipjack tuna and kawakawa were almost unresponsive to temperature. Both rising and falling temperatures produced similar results.

5° C per hour

These experiments provide a rate of temperature change almost the same as used by Stevens & Fry (1972). Because responses of *Euthynnus*-type* species (skipjack tuna and kawakawa) and the yellowfin tuna (*Thunnus*) were markedly different, results are presented separately.

Euthynnids. Regression relationships of log swim speed versus temperature were determined seven times for four skipjack tuna and six times for three kawakawa (Table 3; Figs. 2 and 3). As with 1° C day^{-1} data, standard errors of the estimates were reduced using the log transformation of the swim speed. Each estimate was based on 22–84 laps (every 6th lap is automatically sampled). Values ranged from

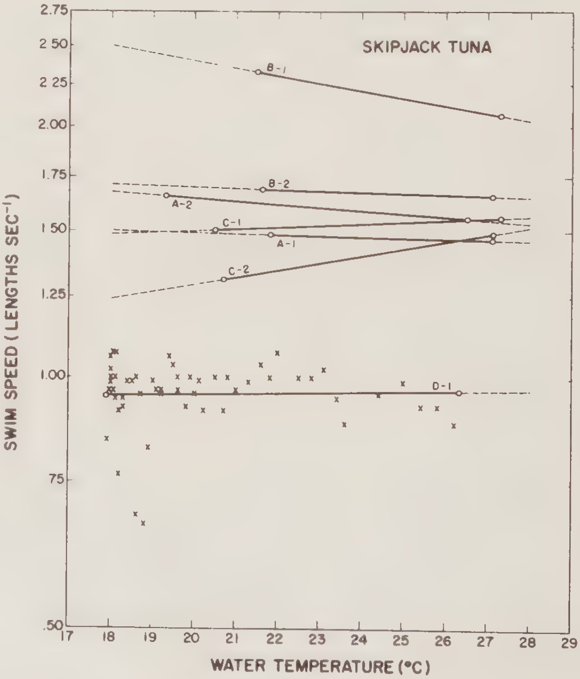

Fig. 2. Influence of temperature changing at about 5° C h^{-1} on the locomotory activity of skipjack tuna. Letters refer to subject, numbers to test sequence. Q_{10}'s were as follows: A (0.98, 0.92); B (0.81, 0.97); C (1.05, 1.22); and D (1.01). X's are sampled swim speeds. Solid lines are regressions of log swim speed on water temperature.

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* Periodically skipjack tuna and kawakawa have been considered cogeneric. Although currently not considered taxonomically precise, we will refer to them collectively as euthynnids.

Table 3. Regression statistics for log swim speed as a function of either ambient temperature (skipjack tuna – SJ or kawakawa – KK) or estimated red muscle temperature (yellowfin tuna – YF). Small letters refer to individuals, numbers to test.

Fish	Fork length (cm)	n	Mean log swim speed (lengths per sec)	Standard deviation	Min. log swim speed (lengths per sec)	Max. log swim speed (lengths per sec)	Regression coefficients a	b	r	Temperature range (° C)
SJa–1	45.5	27	0.167	0.00859	0.161	0.185	0.18977	–0.00092	0.1753	21.8–27.1
–2		42	0.204	0.03282	0.173	0.338	0.28737	–0.00369	0.2569	19.3–26.5
SJb–1	45.0	40	0.340	0.05957	0.233	0.449	0.56119	–0.00906	0.2791	21.5–27.3
–2		30	0.221	0.03251	0.146	0.286	0.25182	–0.00129	0.0700	21.6–27.1
SJc–1	46.5	69	0.181	0.03573	0.086	0.258	0.13096	0.00219	0.1203	20.5–27.3
–2		54	0.135	0.04354	0.000	0.233	–0.06269	0.00866	0.3788**	20.7–27.1
SJd–1	47.0	54	–0.002	0.04093	0.174	0.029	–0.03370	0.00067	0.0380	17.9–26.2
KKa–1	40.7	33	0.314	0.02255	0.279	0.371	0.32599	–0.00057	0.0275	20.9–26.7
–2		45	0.207	0.10221	0.033	0.358	0.97239	–0.03422	0.4855**	20.9–26.5
KKb–1	42.2	39	0.349	0.06122	0.250	0.539	0.76260	–0.01787	0.4681**	21.4–27.4
KKc 1	45.3	57	0.156	0.02698	0.076	0.210	0.29338	–0.00634	0.4451**	19.7–26.0
–2		22	0.072	0.02402	0.025	0.100	0.29423	–0.00958	0.5561**	21.2–25.7
–3		84	0.159	0.02198	0.090	0.223	0.05198	0.00502	0.6261**	17.5–29.0
YFa–1	40.6	28	0.043	0.05537	–0.101	0.160	–0.37285	0.01600	0.7740**	22.1–30.7
–2		37	–0.001	0.08774	–0.102	0.179	–0.84377	0.03330	0.8895**	22.0–28.9
–3		62	0.022	0.10177	–0.103	0.223	–0.84196	0.03592	0.9610**	21.4–28.9
YFb–1	43.4	28	–0.125	0.10472	–0.301	0.031	–1.17840	0.04139	0.8320**	22.0–28.9
–2		33	–0.048	0.08444	–0.210	0.092	–0.98192	0.03650	0.8624**	23.1–28.9
–3		21	0.146	0.07633	–0.091	0.240	–0.27147	0.01646	0.3933	23.0–30.7
YFc–1	56.0	69	–0.012	0.06808	–0.190	0.180	–0.65590	0.02560	0.8832**	20.7–28.9
–2		39	0.024	0.09250	–0.188	0.169	–0.62685	0.02555	0.9293**	20.0–29.0
–3		42	0.070	0.10395	–0.149	0.181	–0.78534	0.03140	0.9313**	20.4–30.9

** = Significant at 0.01.

–0.00906 to 0.00866 (median –0.00906) for skipjack tuna and –0.03422 to 0.00502 (median –0.00958) for kawakawa (Figs. 2 and 3). The slopes were significantly greater than zero for only one of seven skipjack tuna estimates and significantly less than zero for four of the six kawakawa estimates. The results vary greatly among fish and for the same fish among days. Not only did the slopes differ, but swimming speeds at a given temperature varied by a factor greater than two for each species. Regardless of variation, swimming activity did not increase two to three times for a 10° C increase as observed in other species (Prosser & Brown 1961). Rather speed appeared to be constant for skipjack tuna and increased with decreasing temperature for kawakawa.

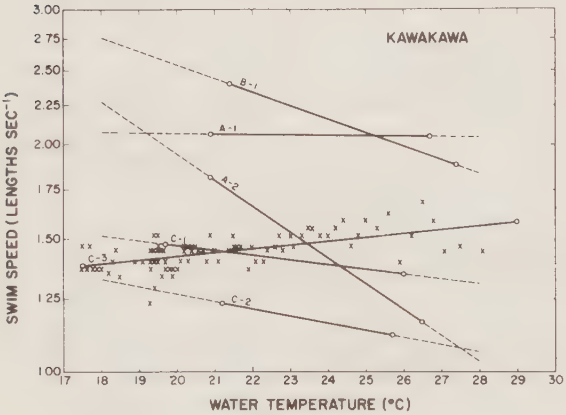


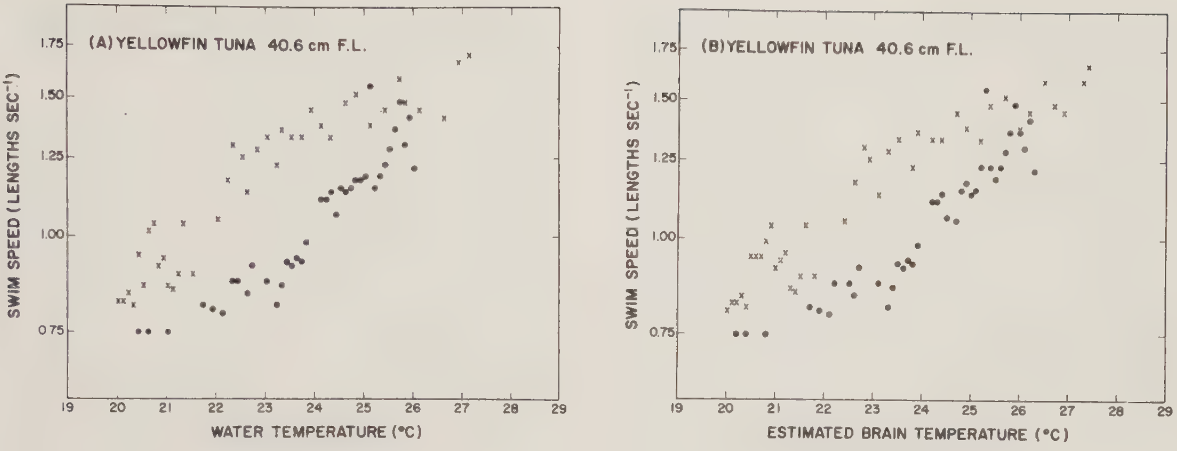
Fig. 3. Influence of temperature changing at about $-5°C\ h^{-1}$ in locomotory activity of kawakawa. Letters refer to subject, numbers to test sequence. Q_{10}'s were as follows: A (0.98, 0.45); B (0.66); and C (0.86, 0.80, 1.12). X's are sampled swim speeds Solid lines are regressions of log swim speed on water temperature.

Thunnus. Regression analysis was performed on nine tests with three yellowfin tuna. Each estimate was based on 21–69 laps (every 6th lap is sampled) (Table 4). These estimates were based on red muscle temperature rather than water temperature because tissue temperatures of the yellowfin tuna lag markedly behind water temperature changes if the latter changes sufficiently fast. Red muscle temperature was estimated by methods outlined in Neill et al. (1976). The importance of this approach can be seen in Figure 4. In Figure 4 log swimming speed is plotted against water temperature of a yellowfin tuna first cooled to about 19° C and then rewarmed the following day. Because swim speed did not decrease as fast as water temperature decreased, the slope of the relationship of the two covariates is initially close to zero. After a delay proportional to the coefficient of temperature change (*k*, Neill et al. 1976), the slope became steeper. The same is observed during the warming on the next day. The resultant hysteresis is obvious. Brain temperature changes slower than changes in the water temperature (Neill et al. 1976) and when speed is plotted against calculated brain temperatures (Fig. 4b) the hysteresis is slightly re-

Table 4. Summary of Q_{10} values estimated for scombrids.

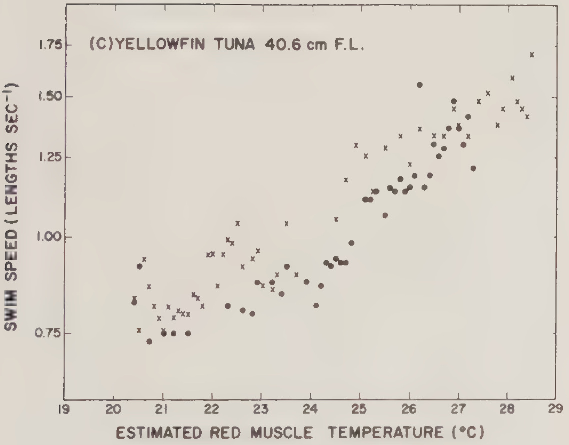
Species	Locomotory activity			Tissue metabolism	Whole animal metabolism
	Rate of temperature change				
	$4°\ C\ h^{-1}$	$5°\ C\ h^{-1}$	$1°\ C\ day^{-1}$		
Euthynnus					
Skipjack tuna	[1] 1.04 (0.96–1.11)	0.98 (0.81–1.22)	1.09	[2] 1.0–1.2	[3] 1.0–1.1
Kawakawa	–	0.85 (0.45–1.12)	1.12	–	–
Thunnus					
Yellowfin tuna	–	2.15 (1.44–2.59)	–	–	–
Bigeye tuna	–	–	–	[2] 1.0–1.2	–

[1] Estimated by us from figure in Stevens & Fry (1972).
[2] Gordon (1968).
[3] Chang, Ito & Neill (see text footnote p. 83).



a

b



c

Fig. 4. Effect of choice of covariate on hysteresis and linearity of temperature-log swim speed plot. X's are swim speeds during cooling. 0's are swim speeds during warming. See text.

duced. But when speed is plotted against calculated red muscle temperature the hysteresis is almost eliminated (Fig. 4c). The relation between speed and temperature observed for yellowfin tuna is mediated apparently by muscle temperature (or some structure that cools and warms at the same rate) rather than by brain temperature or directly by water temperature acting on surface temperature receptors.

It is also apparent from the above that swim speed of yellowfin tuna, in contrast to the euthynnids, is dependent on temperature (Fig. 5). Slopes ranged from 0.01646 to 0.04139 with a median of 0.03140. The slopes of eight of the nine regressions were significantly greater than zero at $P \leq 0.01$.

Discussion

Scombrids can be credited with three compensatory mechanisms with respect to temperature: 1) physiological thermoregulation in which tissue temperatures are maintained at a more or less constant level in spite of variation in external temperature (Barrett & Hester 1964, Cary & Teal 1969, Carey et al. 1971, Stevens & Fry 1971, Graham 1975); 2) behavioral thermoregulation mechanisms, in which the fish can occupy preferred and presumably optional habitat temperatures (Dizon et al. 1974, Dizon, Byles & Stevens 1976, Steffel et al. 1976, Laurs, Yuen & Johnson MS*); and 3) molecular mechanisms of rate-process compensation.

The last category is subdivided by Hazel & Prosser (1974) into a) instantaneous temperature compensation, b) thermal compensation requiring a period of acclimation, and c) compensation over evolutionary time. At the moment, there exists no experimental evidence that individual scombrids possess the ability to acclimate to new temperature environments. Considering their zone of thermal tolerance, there is no reason to suggest that they cannot. Evolutionary thermal compensation has certainly occurred considering the adaptive radiation of tuna species and subspecies through temperate and tropical oceans (Blackburn 1965). Q_{10}'s taken from our study and the literature (Table 4) indicate that euthynnid scombrids do compensate rapidly for changes in temperature. Compensation seems more rapid than in typical temperature acclimation and therefore resembles instantaneous temperature compensation. As a consequence, locomotory activity and metabolism tend to be relatively constant in the face of rapidly changing temperatures. Molecular compensation must be occurring with the observed temperature-independent metabolism (Gordon 1968, Chang et al., see footnote p. 83) and temperature-independent activity is observed for rates of temperature change of 4° C h^{-1}, 5° C h^{-1}, and 1° C day^{-1}; for increasing and decreasing temperatures, and over the entire temperature range (15°–34° C) found to be tolerated by euthynnids. Several exceptions to these statements may be important and should be highlighted.

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* Laurs, R. M., H. S. H. Yuen & J. H. Johnson. Study of the small-scale movements of albacore tuna, *Thunnus alalunga* (Bonnaterre) using ultrasonic tracking techniques. Manuscript in preparation. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92038.

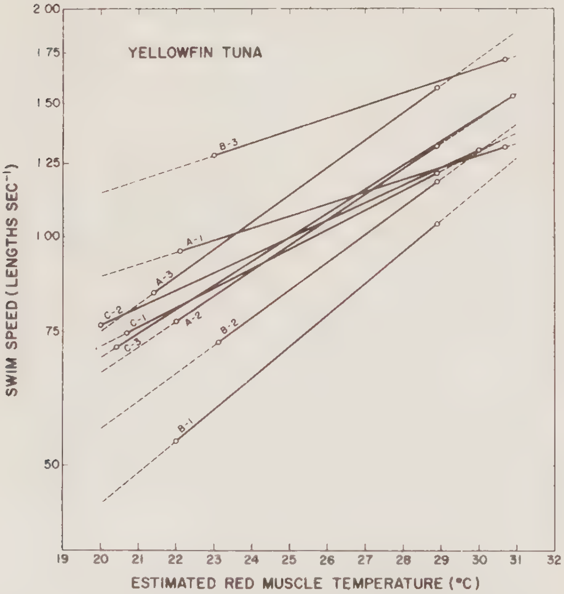

Fig. 5. Influence of temperature changing at about –5°C h^{-1} on the locomotory activity of yellowfin tuna. Letters refer to subject, numbers to test sequence. Q_{10} are as follows: A (1.44, 2.15, 2.24); B (2.59, 2.32, 1.46); and C (1.80, 2.06). Solid lines are regressions of log swim speeds on estimated red muscle temperatures.

First, yellowfin tuna, in contrast to the *Euthynnus* species and to the tissue metabolism of another *Thunnus* (Gordon 1968), have a Q_{10} for locomotory activity similar to nonscombrid fishes (for example *Salmo salar*, see Peterson & Anderson 1969). This is puzzling because they, even more than the *Euthynnus* species, are believed to be fishes of the thermocline and owing to their larger size, could build up higher heat loads with exercise. Both of the above considerations would suggest that yellowfin tuna have greater need for mechanisms of rapid temperature compensation.

One possible explanation for the difference between the yellowfin tuna and the two euthynnids is related to factors dictating continuous swimming as a part of their habits. Scombrids are negatively buoyant, and to maintain hydrostatic equilibrium they must swim at speeds and produce lift on their extended pectoral fins that counters their weight in water (Magnuson 1973). Yellowfin tuna have a gas bladder and large pectoral fins that allow slower minimum speeds than is possible in the euthynnids that have small pectoral fins and no gas bladder. Since yellowfin tuna can swim slower, perhaps they can maintain speeds further above their hydrostatic minimum than can euthynnids and thus have more scope to respond to temperature change. Euthynnids on the other hand may be forced for hydrostatic reasons to swim closer to their maximim endurance speed and thus be less able to respond to temperature changes and, therefore, must need some sort of temperature compensation mechanisms.

Speeds observed in the ring-shaped tank were highly variable, and all three species swam for periods faster and slower than their minimum hydrostatic speeds as calculated by Magnuson (1973) for wild fish. We can only test individual fish in the ring-shaped tank. Tunas of this size are always found in schools and the responses of individuals when prevented from schooling are unpredictable. Removal from their school and introduction into a confining test situation produce degrees of excitement that probably vary among individuals and affects swim speed. While an individual tuna can swim with remarkable speed precision for long periods of time, unexplained and abrupt changes in speed are observed. As yet we are unable to relate these shifts in speed to any observable factors save direction of swimming. Upon reversal in swimming direction, an individual will settle to a new average speed and again maintain it with remarkable precision.

Also contributing to interfish variability is that captive fish lose fat mass, becoming less dense, and can then swim at speeds below minimum. Kawakawa held for long periods (Magnuson 1970) were 40% less dense than wild fish. Some were even 60% less dense in respect to the density of seawater (1.025 g cc^{-1}), with densities as low as 1.049g cc^{-1} compared with the 1.086 g cc^{-1} characteristic of wild fish. Such captivity-induced variations in density could significantly decrease speeds required for hydrostatic equilibrium. Scombrids can also vary the lift coefficient of the pectoral fins (Magnuson 1973) to increase lift, and can incline their bodies at an upward angle of attack to increase lift forces. Fortunately, the observed scope in speed in the ring tank allowed us to assume that both the euthynnids and the yellowfin tuna had the flexibility to respond to temperature change if it had been in their nature; the former did not, the latter did. Secondly, four kawakawa exposed to a 5° C h^{-1} decrease in temperature swam significantly faster at cooler temperatures. This suggests an alarm response to temperatures near their lethal temperature. But skipjack tuna at the same rate of temperature change did not increase their speeds near lethal temperatures. Also kawakawa at 1° C day^{-1} decreased speed near lethal temperature as did skipjack tuna in Stevens & Fry's work. An increased speed near lethal temperatures was not consistent, but if real would be quite functional as it would allow the fish to counteract the cool water by generating more metabolic heat and would remove the fish from a suboptimal area.

Rapid temperature compensation by the euthynnids adds growing evidence of a unique niche filled by skipjack tuna. These tuna with their sensory ability to thermoregulate behaviorally (Dizon et al. 1974, 1976, Steffel et al. 1976), with their countercurrent heat exchanger to damp out short-term temperature change (Neill et al. 1976), and with a metabolism and respiration that is rapidly temperature compensated, possess potent mechanisms to deal with a highly heterothermal environment. Yet, the surface mixed layer of the tropical oceans, generally thought to be the habitat of these tunas, is an environment characterized by little temperature variation. Barkley, Neill & Gooding (MS)* have identified three environmental conditions that should determine distribution for the skipjack tuna: 1) a lower temperature limit – about 18° C; 2) a lower oxygen limit – about 3.5 ml O_2 liter^{-1}; and 3) an upper temperature limit ranging from about 33° C for the smallest commercially sought fish to 20° C for the oldest and largest. These limits may account for the unusual features of their areal distribution and suggest that the actual habitat of adult skipjack tuna is the upper thermocline. Since much forage for the adult tunas is likely to be in the upper mixed layer, frequent forays into warmer, upper waters must be made. Most animals whose metabolism is instantaneously temperature-compensated live in an environment in which temperature fluctuates dramatically (i.e., intertidal forms, Hazel & Prosser 1974). The habitat of the adult skipjack tuna could be similarly constituted. Consider also that they lack a swim bladder, which frees them from effects of changing pressure. Skipjack tuna are thus well suited to exploit fully the environment extending from the upper thermocline to the surface; rapid movements through extremes of temperature and depth pose no particular problems to these highly adapted animals. Rapid temperature compensation contributes to the ability to fill this niche.

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REPRINT FROM
Calif. Fish and Game, 63(2) : 101-116. 1977

FACTORS INFLUENCING DISTRIBUTION OF FISH EGGS AND LARVAE OVER EIGHT 24-HR SAMPLINGS IN RICHARDSON BAY, CALIFORNIA [1]

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To determine the factors affecting the day-night distribution of ichthyoplankton, a series of eight 24-hr samplings was conducted in Richardson Bay, California. Slightly modified channel nets were fished in two locations and collections made for each half-tide stage. Of the different larval taxa collected, *Clupea harengus pallasi, Engraulis mordax* and Gobiidae comprised 98% of the total catch. The most speciose family was Cottidae.

Densities of larvae and eggs were positively correlated with tide stages of the fastest currents and with night conditions. Analysis of the catch results suggests the most determinant factor in the distribution of eggs and larvae is tidal currents.

Interesting occurrences of 10 species of offshore spawned larvae is reported, and a possible explanation for their presence within the bay is discussed.

INTRODUCTION

Ichthyoplankton surveys along the west coast have centered around the CalCOFI (California Cooperative Oceanic Fisheries Investigations) cruises which began in 1949 and concentrated on the ichthyoplankton of the California current (Ahlstrom 1965). Only geographically scattered, recent studies have attempted to understand the inshore, estuarine ichthyoplankton (Eldridge and Bryan 1972; Blackburn 1973; Pearcy and Myers 1974). The only study in the central California coastal area was that of Chadwick (1958) who sampled in the Sacramento-San Joaquin Delta area, upstream from San Francisco Bay. This work dealt principally with the eggs and larvae of striped bass, *Morone saxatilis,* and freshwater species. Pearcy and Myers (1974) are the only researchers to date to study the diel distribution of ichthyoplankton in a Pacific coast estuary. Their study took place over three 24-hr periods, in a comparatively narrow Oregon estuary.

Public and governmental concern over the deteriorating environmental quality of San Francisco Bay principally was responsible for a series of three comprehensive studies which began in 1964 (Pearson, Storrs, and Selleck 1970; Kaiser Engineers 1969; Brown and Caldwell 1971). The main objective of these studies was the evaluation of water quality, primarily the physico-chemical conditions throughout the bay. Research on the finfish population in San Francisco Bay has been limited to juvenile and adult fishes and confined to deeper channel stations (Aplin 1967). Studies were begun by staff members of the Tiburon Laboratory in 1972 in Richardson Bay, a small embayment within San Francisco Bay, to provide comprehensive information on the finfish populations of a shallow, estuarine tidal basin. The project included sampling phytoplankton, ichthyoplankton, and juvenile and adult fishes. Part of the ichthyoplankton survey was

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[1] Accepted October 1976.

concerned with temporal distribution of fish eggs and larvae over short time periods. This work is the subject of the present paper. The major part of the ichthyoplankton survey covered the entire Richardson Bay at weekly intervals over a 1-year sampling period. The results of that survey will be reported later.

Diurnal and nocturnal rhythmic behavior has been documented in adult estuarine fishes (Gibson 1969). Likewise, larvae have exhibited varying diel distribution patterns in open-ocean waters (Isaacs 1964; Bridger 1956) and inshore areas (Lewis and Wilkens 1971; Lewis and Mann 1971; Richards and Kendall 1973; Pearcy and Myers 1974). Since day-night differences in distribution can bias survey results, an effort was made to determine factors affecting distribution of Richardson Bay ichthyoplankton. This paper reports the results of eight 24-hour samplings conducted at two locations from March 23, 1972, to February 9, 1973.

DESCRIPTION OF THE STUDY AREA

Richardson Bay is approximately 11 km (8.0 miles) north of the San Francisco Peninsula (Figure 1). Its total area covers approximately 12.9 km² (4.9 miles²). This surface area changes 10–13% during spring tide conditions indicative of the shallow depth of the bay which averages only 0.45 m (1.4 ft). The only channel of notable depth averages 6m (19.2 ft) and is a minor ship channel adjacent to the city of Sausalito.

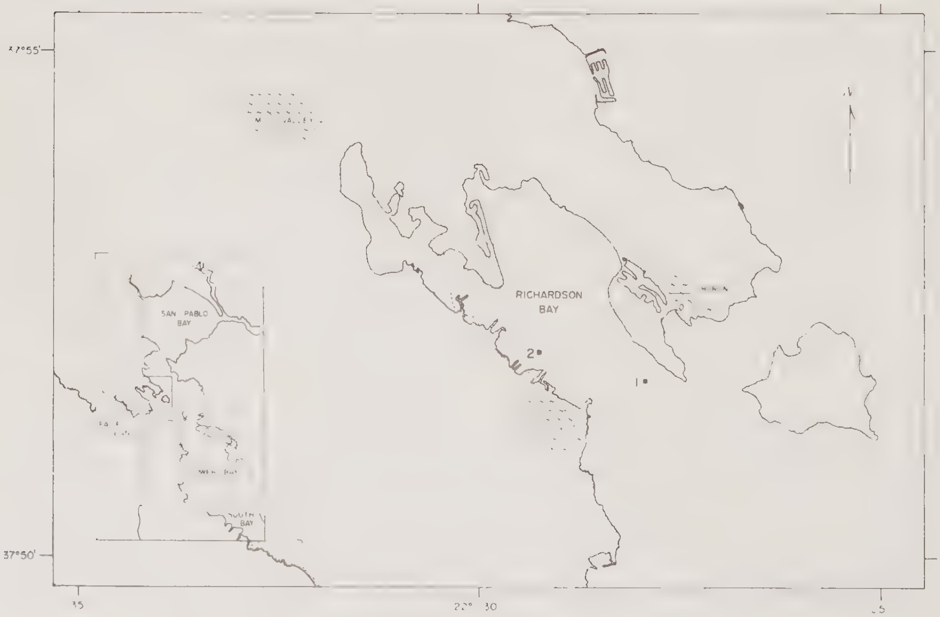

FIGURE 1. Map of Richardson Bay, California, showing the two sampling stations used in the study of the diel distribution of fish eggs and larvae. Short-dashed lines represent the 10-m contours. Long-dashed lines represent water level at zero feet tide level.

Sediment types in Richardson Bay may be described generally as soft marine sediments of "bay mud" with more sandy mixtures in the mud flat drainage channels. Some rocky shore areas are located near the entrance to the bay.

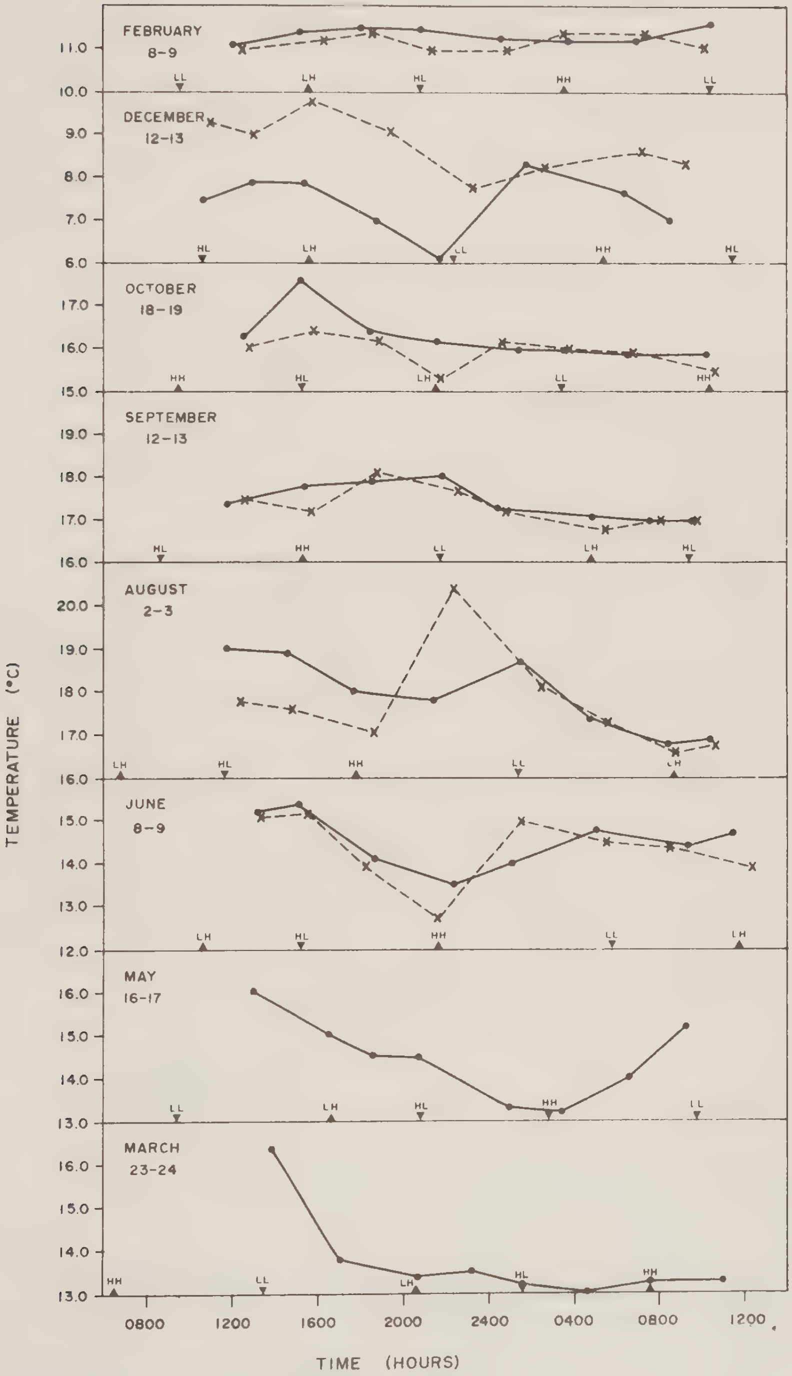

FIGURE 2. Water temperature measured in the study of fish eggs and larvae of Richardson Bay, California. Solid line represents Station 2 and dotted line Station 1. Different tide stages are indicated by triangles with appropriate symbols (LL = lower low tide; HL = higher low; LH = lower high; HH = higher high).

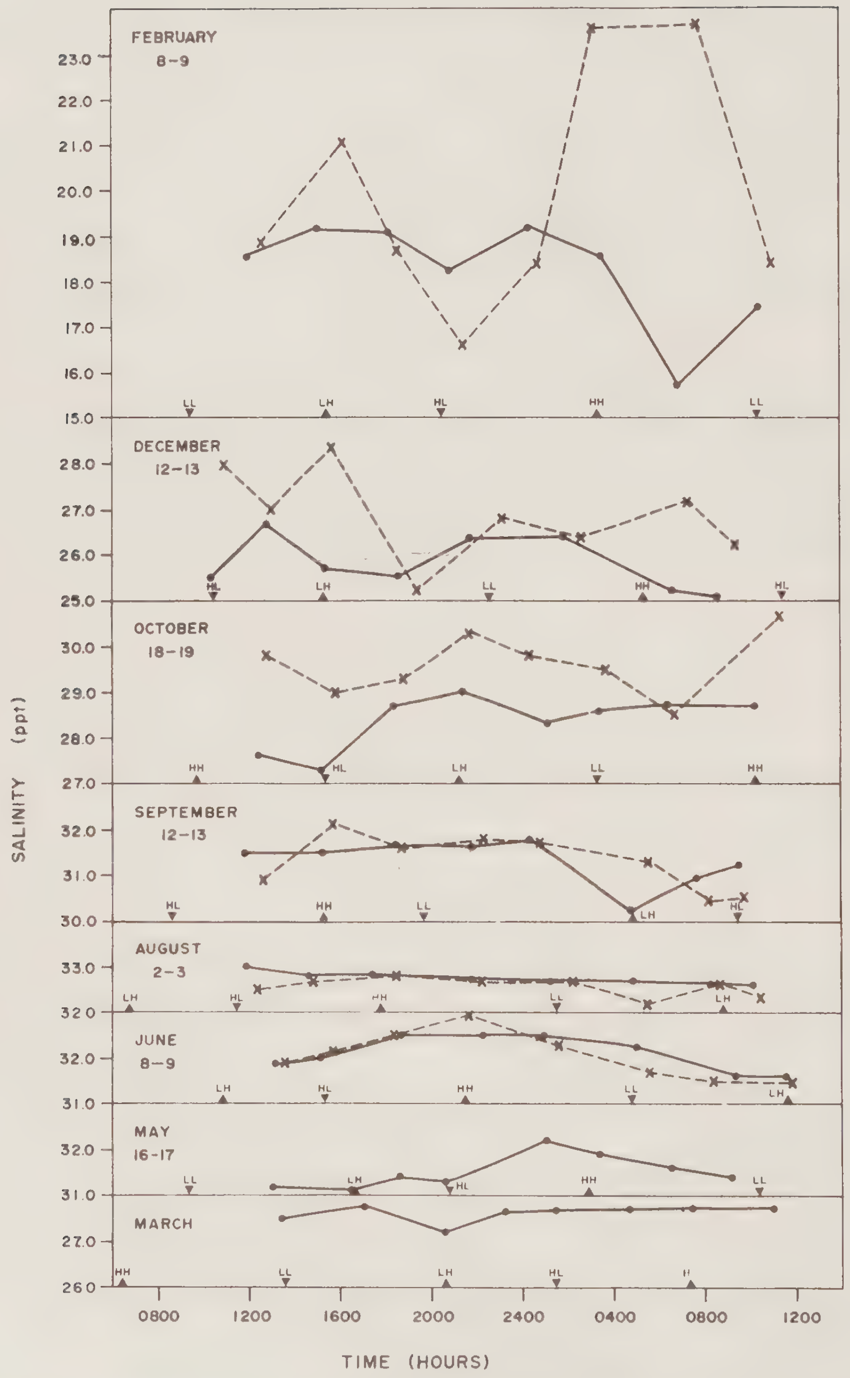

FIGURE 3. Salinities measured in the study of fish eggs and larvae of Richardson Bay, California. Solid line represents Station 2 and dotted line Station 1. Different tide stages are indicated by triangles with appropriate symbols (LL = lower low tide; HL = higher low; LH = lower high; HH = higher high).

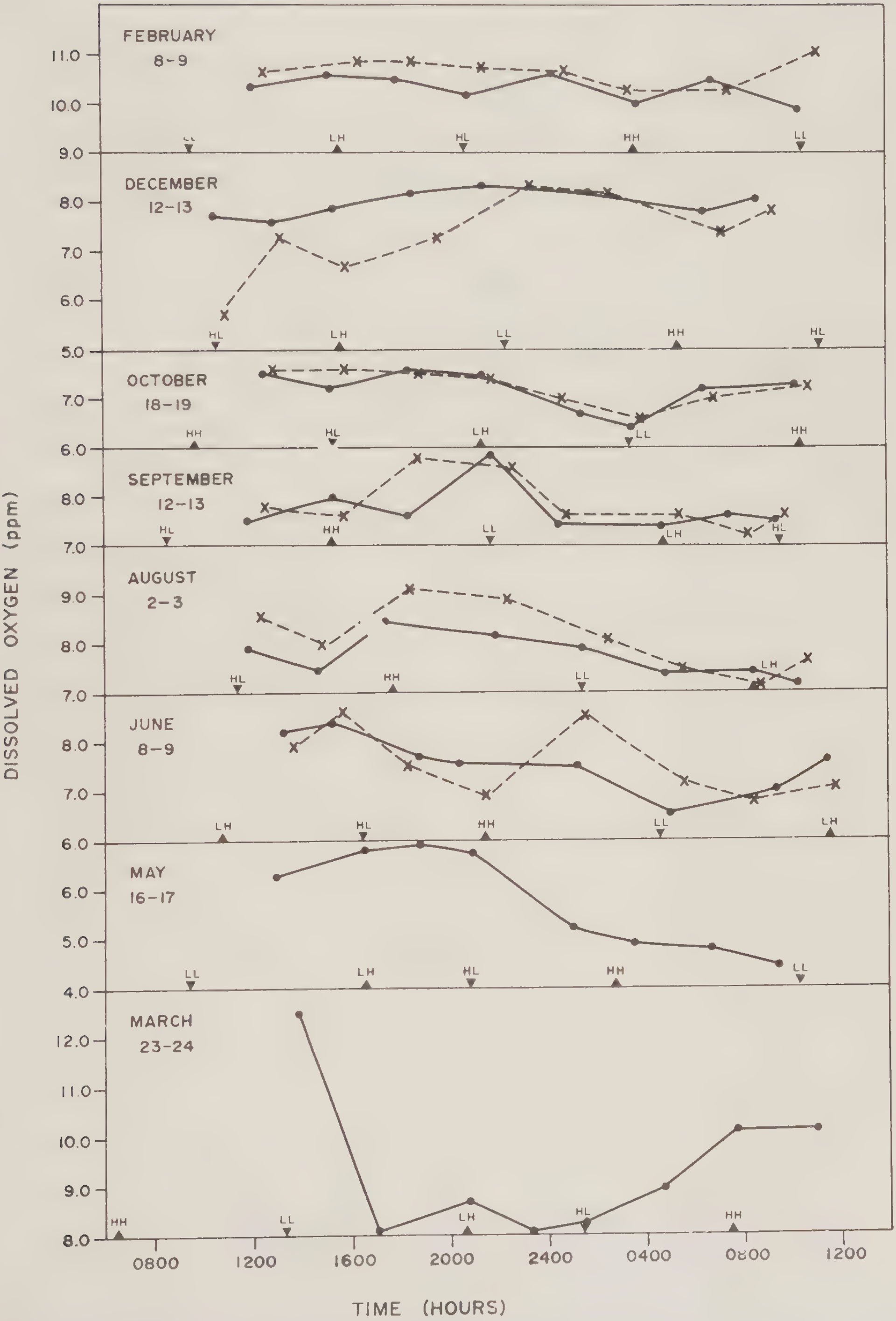

FIGURE 4. Dissolved oxygen concentrations measured in the study of fish eggs and larvae of Richardson Bay, California. Solid line represents Station 2 and dotted line Station 1. Different tide stages are indicated by triangles with appropriate symbols (LL = lower low tide; HL = higher low; LH = lower high; HH = higher high).

Frolander (1964) considered an estuary to be two-layered or stratified when conductivity, as a measure of salinity, changed by four or more units within a 1-m (3.3-ft) depth. By that definition Richardson Bay would be considered a vertically well-mixed estuary. Only during periods of high winter rainfall, near the entrance to the bay, did any evidence of stratification occur. Freshwater inflow into the bay comes mainly from two small creeks which drain a watershed area of approximately 45.7 km^2 (17.6 miles^2). Also two sewage treatment plants discharge 11.67 × 10^8 gallons of primary treated effluent per year into the bay.

Temperature, salinity, and dissolved oxygen levels were monitored throughout the sampling period (Figures 2, 3, and 4). The overall physico-chemical conditions were a function of the tide, season, and freshwater runoff. In winter the marine water entering the bay tended to moderate the colder, turbid upstream water. Conversely, in summer upstream water temperatures were generally warmer, and salinities were at their annual highs. At times the bay became a "hypersaline" or "negative" type estuary as described by Frolander (1964).

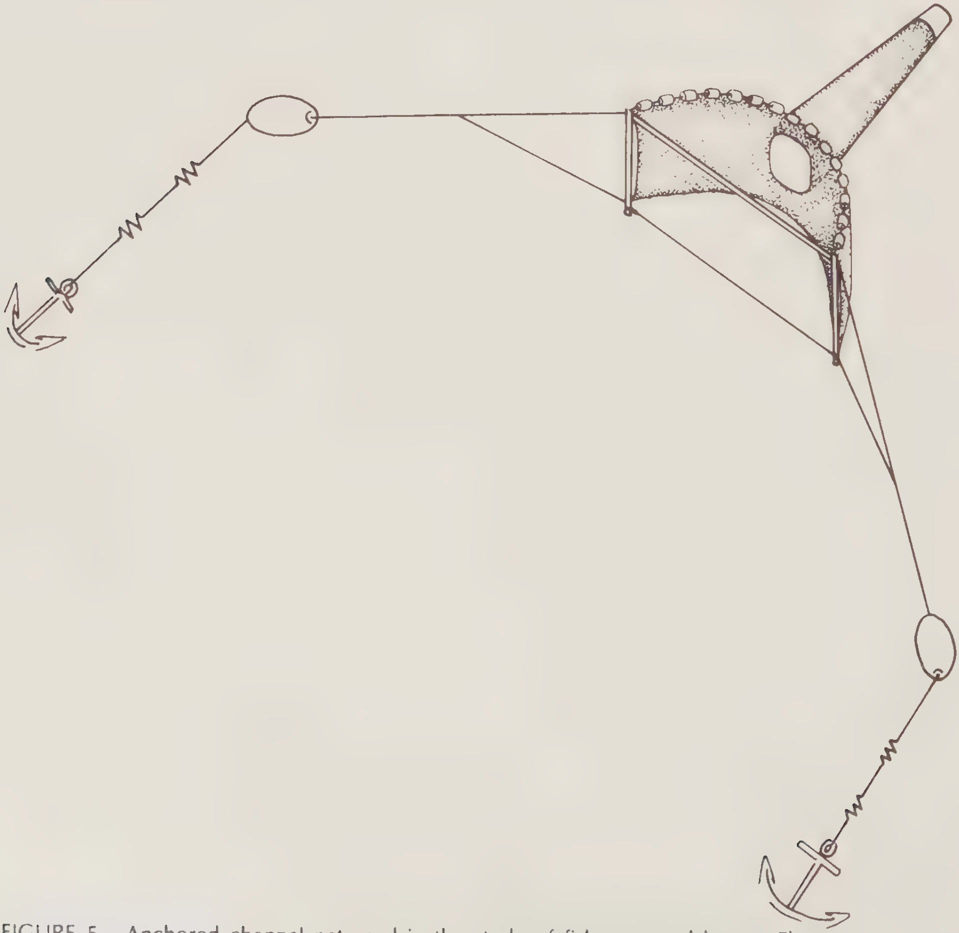

FIGURE 5. Anchored channel net used in the study of fish eggs and larvae. Flow meter (not shown) was mounted eccentrically in round 0.5 m net opening.

METHODS

Sampling of the ichthyoplankton was carried out during eight 24-hr periods (Table 1) using a modified version (Figure 5) of a channel net (Lewis, et al. 1970). The net was fished in a stationary position, anchored in place, facing the tidal current. The tail bag consisted of a 0.5-m (1.7-ft) plankton net of 333 μ mesh. The wing dimensions were approximately 1 x 3-m (3.3 x 9.9 ft) with ⅛-inch square nylon webbing. Digital flowmeters (Model 2030, General Oceanics, Inc.[2]) were mounted eccentrically in the mouth of each net to estimate the amount of water filtered. In the samplings of May 16, 17 and February 8, 9, numerous difficulties were encountered, i.e., clogging of the flowmeters, malfunctions, etc. Because many volume measurements of these two studies were questionable, I decided not to use the data for comparisons of catch (numbers of larvae/m^3). Nets were placed in two locations in Richardson Bay (Figure 1); one in the ship channel in the middle part of the bay (Station 2), and the other near the entrance (Station 1). The water depths ranged from 1.0 to 2.0 m (3.3 to 6.6 ft) at Station 2 and 2.0 to 4.4 m (6.6 to 14.5 ft) at Station 1. For the first two studies (March 23–24 and May 16–17) only Station 2 was fished. To remove bias with respect to time (and weather conditions) the sampling dates were randomly selected ahead of time by means of a random numbers table, choosing two dates per season.

The sampling schedule for each 24-hr period was divided according to tide stages; the objective being to sample separately the first and second halves of each tide stage (Figure 6). The net was allowed to fish for the entire half-tide stage, then it was washed down, the plankton sample removed, and the net replaced for the next half-tide stage. For simplification in the succeeding text,

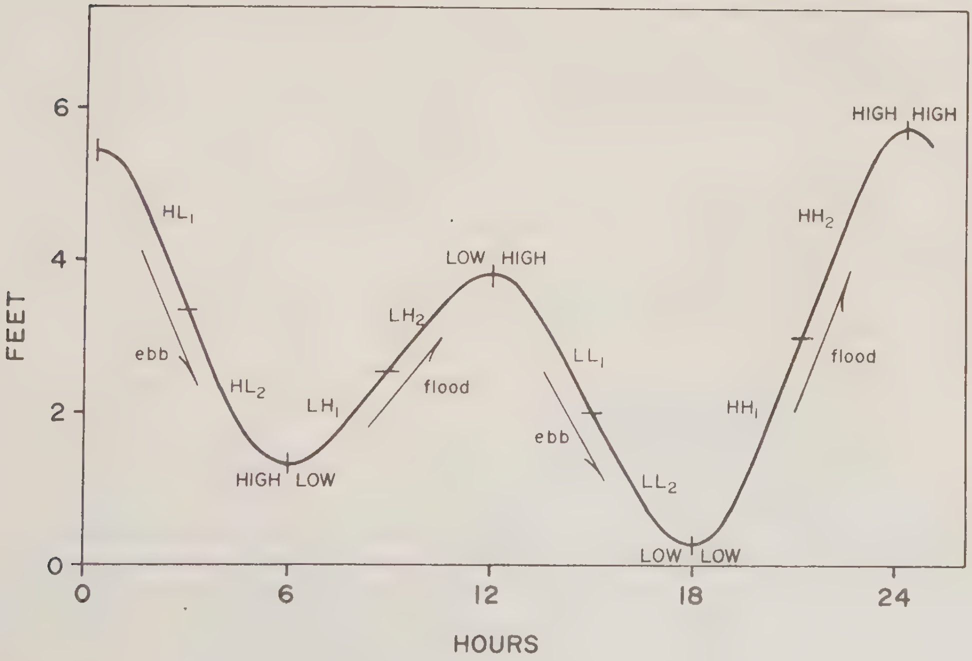

FIGURE 6. Typical tide curve and coding of sampling periods used in each 24-hr study.

the different half-tide stages are represented as follows: high high tide stage = HH_1 (first half) and HH_2 (second half); low high = LH_1 and LH_2; high low = HL_1 and HL_2; and low low = LL_1 and LL_2.

Concurrent to net samplings, the following physico-chemical parameters of bay water were measured: dissolved oxygen, temperature, salinity, pH, and turbidity. Vertical profiles of all parameters were made in front of each net. The values presented in Figures 2, 3, and 4 represent measurements taken in the mouth of each net. The ichthyoplankton samples were preserved in 5% buffered formaldehyde. Processing of samples followed procedures described by Kramer (Kramer, et al. 1972).

Component factor analyses (Rummel 1970) were used to determine the different relations between dependent and independent variables. This statistical method first calculated a correlation coefficient matrix of all possible combinations of variables. Then by matrix rotation it organized groups of related variables into distinct factors, which are independent of each other. Combined data for the entire year and data within each study were analyzed in this manner. Related variables were subsequently analyzed by analysis of variance.

RESULTS

Species Composition and Abundance

Among the eight different sampling periods a total of 38,226 larvae were caught, representing 39 separate taxa (Table 1). Twenty-six larval types were identified to species. Of the remaining larvae, two were identified to genus and 11 to family. *Clupea harengus pallasi* (Pacific herring), *Engraulis mordax* (northern anchovy), and Gobiidae larvae comprised 98% of the total catch. The next most abundant types were *Cynoscion nobilis* (white seabass), *Leptocottus armatus* (staghorn sculpin), and *Hypsopsetta guttulata* (diamond turbot).

The most speciose family was Cottidae (seven species) followed by Pleuronectidae with five species. Large catches which occurred mostly in the fall and winter studies were due to Pacific herring spawning. When the herring were not spawning, Gobiidae replaced them as the most abundant type. Gobiid 1, the unidentified Gobiid larvae, was the only type caught in all eight samplings.

Temporal Distribution

Results of factor analysis and correlation analyses of all eight studies combined throughout the year showed the following significant relations between variables within factors:

i. the number of larvae positively correlated ($P = .05$) with ebbing tides.
ii. the number of species showed a significant ($P = .01$) increase on ebb tides.
iii. the catch (number of larvae/m^3) was significantly ($P = .05$) higher during ebb tide conditions.

Within individual 24-hr samplings similar analyses indicated varying results. During March ebb tides the plankton volumes and the number of species were the highest. The catches (number of larvae/m^3) in June consisted mostly of Gobiidae. The number of eggs and the number of species were directly related to catch (number of larvae/m^3). In August, during flood tides, the number of species and the number of eggs increased, and the catches of *Hypsopsetta*

TABLE 1. Numbers of Larvae of Different Fish Species Caught According to Location (Station 1/Station 2), date, and half tide stage.

Taxa	*March*	*May*	*June*	*Aug.*	*Sept.*	*Oct.*	*Dec.*	*Feb.*	*LL*		*HL*		*LH*		*HH*		*Total*
	23, 24	*16, 17*	*8, 9*	*2, 3*	*12, 13*	*18, 19*	*12, 13*	*8, 9*	*1*	*2*	*1*	*2*	*1*	*2*	*1*	*2*	
Clupeidae																	
Clupea harengus pallasi	–/1094						857/14,800	171/3,795	2,116	1,860	291	746	218	51	9,346	89	20,717
Engraulidae																	
Engraulis mordax	–/4			114/20	95/72	95/72	1,810/65	365/27	1,097	349	480	501	29	56	58	135	2,705
Osmeridae																	
Spirinchus thaleichthys			1/0				1/0		2								2
Allosmerus elongatus								1/0	1								1
Osmerid 1	–/6				0/1			1/1	1	3	1	2	1	1			9
Osmerid 2			1/0											1			1
Batrachoididae																	
Porichthys notatus						0/1	2/0		1	1		1					3
Ophidiidae																	
Brosmophycis marginata			2/0	2/0					2					2			4
Atherinidae																	
Atherinopsis californiensis	–/1			1/0			1/0			2		1					3
Atherinops affinis						0/3	9/3		1	10			2		2		15
Syngnathidae																	
Syngnathus leptorhynchus					1/1	13/23	4/1	1/0	27	10		1	1	4	1		44
Sciaenidae																	
Cynoscion nobilis	–/1				1/0	37/17	9/3	54/5	67	7		18	2	3	21	9	127
Embiotocidae																	
Cymatogaster aggregata				1/1								1	1				2
Clinidae																	
Clinid 1	–/1		1/0					1/0	2	1							3
Clinid 2								1/2	1			1			1		3
Stichaeidae																	
Stichaeid 1		–/1			3/0	1/0			1			3	1				5
Stichaeid 2								1/0				1					1
Pholidae																	
Pholid 1								1/0				1					1
Ammodytidae																	
Ammodytes hexapterus								7/0	4			2			1		7

TABLE 1. (Continued)

Taxa	March 23, 24	May 16, 17	June 8, 9	Aug. 2, 3	Sept. 12, 13	Oct. 18, 19	Dec. 12, 13	Feb. 8, 9	LL 1	LL 2	HL 1	HL 2	LH 1	LH 2	HH 1	HH 2	Total
Gobiidae Clevelandia ios					0/3	0/4	0/25		1	3		1	3		23	1	32
Ilypnus gilberti					0/3								3				3
Gobiid 1	–/2,412	–/1,193	257/34	922/1,260	1,553/895	2,180/2,055	548/299	331/248	4,781	2,975	1,097	706	1,772	1,345	1,274	237	14,187
Stromateidae																	
Peprilus simillimus						1/0									1		1
Scorpaenidae																	
Sebastes spp.				1/0		4/1	14/6	20/1	10	12	9	7	2		5	2	47
Hexagrammidae																	
Ophiodon elongatus								7/0	4	1		2					7
Cottidae																	
Scorpaenichthys marmoratus								4/0	1	1						2	4
Leptocottus armatus	–/21				0/1	1/0	38/14	40/6	46	16	25	5	7	5	13	4	121
Oligocottus maculosus	–/2						4/0	2/0	1		1	4	2				8
Oligocottus snyderi						1/0			1								1
Cottid 1						0/1									1		1
Cottid 2							2/1					1	2				3
Cottid 3								2/1	1	1		1					3
Bothidae																	
Paralichthys californicus						11/0			10	1							11
Citharichthys spp.				0/1	7/1	6/6		0/1	6	1	2		6	1	5	1	22
Pleuronectidae																	
Lyopsetta exilis								1/0				1					1
Parophrys vetulus								1/0	1								1
Hypsopsetta guttulata			1/0	6/13	5/3	24/17		1/0	36	5	2	3	4	12	10	8	80
Platichthys stellatus	–/5			0/2						1	1		2	1		2	7
Psettichthys melanostictus								38/5	6	10		3	23		1		43
Total									8,228	11,269	1,910	2,015	2,077	1,484	10,763	490	38,236

guttulata were higher. Larval catches in number of larvae/m³ correlated directly with the Gobiidae and *Engraulis mordax.* Catches of December's and February's samplings were comprised mostly of *Clupea harengus pallasi* and the highest numbers were caught during HH_1 stage. The greatest number of species (14 taxa) occurred on the LL_1 stage in February.

TABLE 2. Summary of Number of Larvae, Percentage of Total Catch, and Catch in Number of Larvae/m³ According to Tide Stage

	Ebb				*Flood*			
	LL_1	LL_2	HL_1	HL_2	LH_1	LH_2	HH_1	HH_2
No. of Larvae	8,828	11,269	1,910	2,015	2,077	1,484	10,763	490
Percent of Catch	21.5	29.5	5.0	5.3	5.4	3.9	28.1	1.3
No./m³	6.109	11.262	1.761	1.458	5.030	1.479	9.926	.439

An examination of the results for the entire year according to half-tide stages (Table 2) demonstrates that both highest numbers of larvae captured and the highest density of larvae took place in LL_2, HH_1 and LL_1, respectively. Combin-

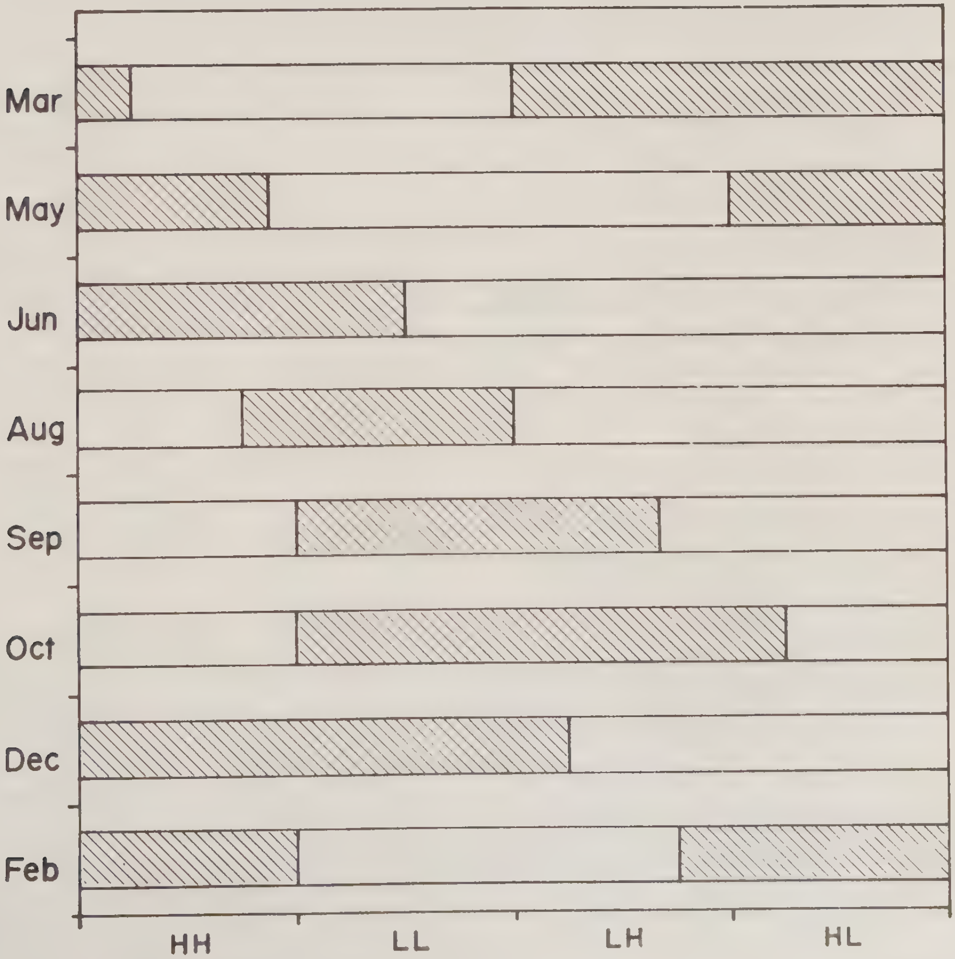

FIGURE 7. Relative amount of day and night conditions according to tide stage and individual 24-hr sampling. Hash marked portions represent night

ing the catches of the two halves of each tide stage, 51% of all larvae were taken at the LL tide stage. These results indicate that larval densities were highest during the periods of high current, either HH flood or LL ebb.

In six of the eight 24-hr samplings in which accurate density measurements could be compared, much greater larval densities occurred during night conditions than in daylight (Table 3). The LL stage usually occurred at night (Figure 7). Two exceptions to these concurrences were March and June's samplings. Low low tide (LL) happened during daylight hours in March, and one-half of June's LL tide occurred during daylight. Interestingly enough, the only times when there were greater larval fish catches during the day were in March and June. This suggests that larval densities were related to current velocities. There is also a demonstrated positive relation between density and night condition.

TABLE 3. Comparison of Larval Fish Catches (Number of Larvae/m^3 at Night Versus Day)

	March	*May*	*June*	*August*	*Sept.*	*Oct.*	*Dec.*	*Feb.*	*Overall Average*
Day	3.1517	–	0.791	0.4889	4.0960	0.5393	1.1098	–	1.4612
Night	2.2138	–	0.6315	3.4370	7.330	13.7850	10.9410	–	7.2566

Conclusions about seasonal distribution of eggs and larvae must be considered preliminary and generalized due to the infrequency of sampling with only two samples per season. The number of species was greater in the winter samples. Winter sampling times were characterized by periods of high fresh-water inflow and precipitation, low water temperatures, low salinities, and high dissolved oxygen concentrations. The catch also was highest in winter during the periods with the greatest tide range.

Spatial Distribution

Only limited conclusions can be drawn about spatial distribution because of infrequent sampling and because Station 2 only was fished in the March and May studies. In the six paired studies, more species were collected at Station 1, near the entrance of the bay. Higher catches of specific fishes occurred as follows:

i. In June more *Citharicthys* spp., and *Hypsopsetta guttulata* were found at Station 1.
ii. In September, both the catch and the number of species were higher at Station 1.
iii. October and February's studies showed higher catches of *Sebastes* spp., and *Scorpaenichthys marmoratus* at Station 1.

Individual Species

Clupea harengus pallasi—Adult *C. h. pallasi* historically have entered San Francisco Bay for spawning from November through March, and they spawn on the rocky shorelines near the entrance to Richardson Bay (Eldridge and Kaille 1973). I have noted the demersally spawned eggs on vegetation in upstream portions of the bay as well, but these spawnings were minor in both density and area of spawn. Catches of larvae occurred only during winter months (March, December, and February) and were correlated with the lowest temperatures recorded in all 24-hr samplings. The highest numbers of *C. h. pallasi* were caught on HH_1 (Table 1), indicating that the larvae were carried in on flood tides from areas outside or adjacent to Richardson Bay.

Engraulis mordax—Pelagic eggs of *E. mordax* have been collected every month of the year in the California current (Frey 1971) with peaks of abundance in late winter and early spring and another minor peak in early fall. Adult *E. mordax* normally are found in San Francisco Bay in greatest abundance from midsummer through early fall. Larvae were netted in samplings from August through March. The highest density occurred in December. The majority (91%) of larvae were captured at Station 1, suggesting that the main spawning occurred outside or near the entrance to Richardson Bay.

Gobiidae—A minimum of seven gobiid species have been known to inhabit San Francisco Bay (Aplin 1967; Ruth 1969; U.S. Fish and Wildlife Service 1970; Green 1975). There was difficulty in identifying this study's gobiid larvae because of a limited number of larval descriptions and the overlap of larval characters. Although most of the goby larvae could not be identified with certainty to species, the majority were very likely *Clevelandia ios,* the most commonly found goby in Richardson Bay.

Gobiid larvae comprised the only taxon found in all eight studies. They were also evenly distributed between the two stations (52% of all gobiid larvae were from Station 1). Over half (54%) of all Gobiidae were caught on LL ebb tide.

Others—Both *Syngnathus leptorhynchus* and *Leptocottus armatus* are common, year-round residents of San Francisco Bay. Both species of larvae were caught in the LL ebb currents (85% and 78%, respectively). There have been eight species of adult *Sebastes* caught in San Francisco Bay (Ruth 1969). Their larval presence in Richardson Bay was seasonal (all but one in October, December, and February) and they evidently entered the small bay from outside; 83% of all *Sebastes* larvae were from Station 1.

Three fishes (*Cynoscion nobilis, Hypsopsetta guttulata, Psettichthys melanostictus*), which most likely spawn pelagic eggs outside San Francisco Bay, were netted in fair numbers (Table 1) in Richardson Bay. *Cynoscion nobilis* and *Psettichthys melanostictus* were caught principally at Station 1 (72% and 88%, respectively) while *Hypsopsetta guttulata* appeared more generally dispersed between the two stations. In no San Francisco Bay surveys, to my knowledge, have sexually ripe adults of these three species been found.

DISCUSSION

From the catches of all larvae and individual species, and from plankton volumes and numbers of species, it appears that the single most influential factor determining the density of fish larvae was tidal current. The highest larval densities occurred when tidal currents were the fastest; that is, on LL ebb and HH flood (Table 2). The fact that larval fish catches were markedly higher at night would appear to conflict with the tidal factor until one realizes the concurrence of strong LL ebb currents and night conditions. It is altogether likely and probable that light is a factor affecting distribution of larval fishes. Lewis and Wilkins (1971) found occurrences of three estuarine fishes (*Leiostomus xanthurus, Brevoortia tyranus,* and *Logodon rhomboides*) had highly significant relations with the amount of light and tidal currents. Results of this study, however, indicate that between tidal and light factors tidal influence is more determinant with regard to distribution of fish eggs and larvae.

Associations of larvae with various physico-chemical parameters were found to correspond with variables which characterized either an upstream water mass being carried out with ebb tide or outside marine water entering with flood tide. For instance, May's flood tide water was associated with high salinity, low temperature, and high amounts of stratification detected in vertical profiles. In winter, December's lower salinity and temperature values occurred on ebbing tides. This resulted from heavy runoff from local rains and low air temperatures.

An interesting correlation which arose was a highly significant ($P = <.01$) negative correlation between the number of species and the coastal upwelling index. The indices used in this comparison are those described by Bakun (1973). A negative upwelling index signifies downwelling of surface water at the coast and a net shoreward movement of surface water. Coastal upwelling values were obtained from NMFS, Pacific Environmental Group (Monterey, California) and averaged for the 2-week periods prior to each study date. The types of larvae which were associated with negative upwelling indices are those which were most likely spawned offshore or, at least outside the entrance to San Francisco Bay. They were: *Cynoscion nobilis, Sebastes* spp., *Paralichthys californicus, Citharichthys* spp., *Lyopsetta exilis, Parophrys vetulus, Hypsopsetta guttulata* (weakly associated), *Platichthys stellatus,* and *Psettichthys melanostictus.* Four of these species were caught in such small numbers, it is most likely their presence is a fortuitous occurrence. This is especially true for *Peprillus simillimus* whose population centers off southern California (Hart 1973).

Although there have been few larval fish studies along the estuaries and coastal areas of the U.S. Pacific coast, two surveys (Eldridge and Bryan 1972; Pearcy and Myers 1974) compare well with this study in terms of species composition and catch (Table 4). *Clupea harengus pallasi,* gobiid and cottid species appeared abundant in all three locations, and *Cottidae* was the most speciose family. *Engraulis mordax* is the single most abundant adult fish both in biomass and individual numbers in San Francisco Bay (Aplin 1967). The pelagic eggs and larvae were evidently not a major constituent of the ichthyoplankton in the other, more northern bays.

TABLE 4. Results of Three Larval Fish Studies in Estuaries of the Pacific North Coast Area of the United States

	Number taxa	*Number families*	*Most speciose family*	*Three most abundant taxa*
Richardson Bay, California (Eldridge 1977)	39	20	Cottidae	*Clupea harengus pallasi* *Engraulis mordax* *Gobiidae*
Humboldt Bay, California (Eldridge and Bryan 1972)	37	17	Cottidae	*Lepidogobius lepidus* *Clupea harengus pallasi* *Leptocottus armatus*
Yaquina Bay, Oregon (Pearcy and Myers 1974)	45	17	Cottidae	*Clupea harengus pallasi* *Lepidogobius lepidus* *Cottus asper*

The limited scope of this particular study in space and time does not permit any conclusions regarding the degree or extent of dependence on the estuary by fishes. Results show that at least 39 different fish taxa including many species with offshore dwelling adult stages, were present in the bay. Among the three most abundant larval types, *C. h. pallasi* and *E. mordax* spawned in or near Richardson Bay and represent commercially fished species. Pearcy and Myers

(1974) concluded that although Yaquina Bay was an important nursery for the young of several marine fish species, their larval fish survey showed only *C. h. pallasi* to be abundant. This study's results differed principally in the relative abundance of *E. mordax.* An extensive survey conducted in oceanic areas adjacent to San Francisco Bay and simultaneous sampling inside the bay would establish whether the center of the anchovy population was located in the bay or outside.

ACKNOWLEDGMENTS

Each 24-hr study required a minimum of six persons. The working conditions were often uncomfortable, the hours long, and the weather inclement.

I especially appreciate the assistance given by Roger Green, Paul Wares, Lloyd Richards, and Jeffrey O'Neill. Elbert H. Ahlstrom and his staff provided help with larval identifications, and Jeannette W. Struhsaker assisted with the data analyses. Helpful manuscript reviews were provided by E. H. Ahlstrom, Arthur W. Kendall, and Sally L. Richardson.

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Vol. 106, No. 5, September 1977
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Energetics of Pacific Herring (*Clupea harengus pallasi*) Embryos and Larvae Exposed to Low Conentrations of Benzene, a Monoaromatic Component of Crude Oil

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ABSTRACT

Interest in the energetic processes of critical early life stages of Pacific herring (*Clupea harengus pallasi*) and the potential effects from sublethal exposure to benzene, a monoaromatic component of crude oil, led to a series of experiments which examined metabolism of herring embryos, yolk-sac larvae, and post-yolk-sac larvae. Yolk caloric content was 6,020 cal/g or 1.3 calories per egg. This energy was consumed rapidly during incubation; total yolk absorption occurred 12 days after fertilization. Anabolic rates varied but at no time was there an energy deficit. Oxygen consumption of embryos increased prior to hatching, then a 10-fold rise was seen in newly hatched yolk-sac larvae. Exogenous calories were estimated from ingested rotifers and were less definable than endogenous energy due to variable grazing rates. Sublethal concentrations of benzene caused (a) significantly less embryonic tissue growth, (b) significantly different oxygen consumption in embryos, and (c) significantly greater assimilation in feeding larvae. It is believed activity of larvae played an important role in accounting for increased metabolism of later stages.

When fish eggs and larvae are viewed as open systems through which energy enters and exits (Von Bertalanffy 1950), they exhibit unique differences from older life stages. Eggs, embryos, and yolk-sac larvae rely solely on endogenous energy sources in their primary energy expenditures for growth and development. Later larval stages must obtain energy from exogenous food sources. Near yolk absorption, larvae must develop to the stage where they can successfully make the transition to exogenous energy utilization by locating, capturing, and metabolizing food (see "critical period," May 1974). Survival of these early life stages is often tenuous, and an understanding of the energetic processes and the environmental and inherent factors affecting them is ecologically important.

In addition to naturally occurring environmental stress on early stages, there are stresses resulting from man's alteration of the environment, such as pollution. Among the increasing hazards to fish eggs and larvae in this regard is the potential exposure to crude oil and petroleum products. Eggs and larvae of phylogenetically divergent species have exhibited lethal and sublethal responses when challenged with crude oil, oil dispersants, and oil/dispersant mixtures (Chipman and Galtsoff 1949; Mironov 1967, 1969; Kühnhold 1969, 1972, 1974; Wilson 1970; Lindén 1974, 1975, 1976). Our studies on effects of petroleum hydrocarbons on fishes have emphasized the critical early life stages and single oil components among the more toxic aromatic fractions of crude oil. In most experiments we tested the effects of benzene, a principal aromatic component of crude oil (Anderson et al. 1974) which is relatively water-soluble (Benville and Korn 1974), highly lipid-soluble, and is toxic to Pacific herring eggs and larvae in initial exposure concentrations from 5 to 50 μl/liter (Struhsaker et al. 1974).

Considerable research has been done on the energetics of fish larvae in relation to the "critical period" (Lasker 1962; Toetz 1966; Laurence 1969; Cooney 1973; May 1974). In addition, several researchers have defined the effects of varying physical-chemical conditions, primarily temperature and salinity, on various metabolic parameters and energy utilization (Holliday et al. 1964; Blaxter and Hempel 1966). Little work, however, has been done on the effects of oil pollutants on metabolism and energy utilization of early stages.

The research reported here had three objectives: (1) to outline the energetics of

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[1] Formerly J. A. Struhsaker.

TABLE 1.—*Independent variables in benzene toxicity experiments with Pacific herring.*

Experiment	Developmental stage	Duration of experiment (after fertilization)		Exposure times	Mean initial benzene concentration (μl/liter)			Mean temperature (C)	Mean salinity (‰)
		Days	Hours		Control	Low	High		
1	Embryo	0–7	0–168	Initial exposure only	0	0.06	0.56	13.5	23.0
2	Yolk-sac larva	7–12	168–288	Initial exposure only	0	0.04	0.52	12.5	23.0
3	Post-yolk-sac larva	12–24	288–576	Initial exposure only	0	0.14	2.10	12.2	23.0

Pacific herring eggs and larvae; (2) to demonstrate effects, if any, of exposure to sublethal concentrations (approximating chronic levels) of benzene on various energetic parameters: and (3) to contrast the energy budgets of larvae in the above experimental conditions.

METHODS

Three individual experiments were conducted, each concerned with a different early life stage—embryo, yolk-sac larva and post-yolk-sac larva.

For experiments on embryos we needed to establish the exact time of fertilization, and to expose the embryos as soon as possible after fertilization. To do this, sexually mature Pacific herring were collected from San Francisco Bay in December 1974, and artificially spawned in the laboratory. Eggs were extruded by stripping, and distributed in single-egg rows on 10 × 25 cm clear glass plates. The plates were immersed in containers filled with a milt-seawater mixture for about 1 min. The plates were then rinsed in triple-Cuno[2] filtered (pore size 5 μ) seawater and placed in rectangular 8-liter test containers.

For experiments on larvae, test organisms were obtained from naturally spawned eggs collected within 24 h after spawning in San Francisco Bay. The eggs from two different spawns (December 1974 and January 1975) were used in the yolk-sac and post-yolk-sac larva experiments. Eggs were rinsed after being brought from the field and placed in the same 8-liter test containers for incubation. Larvae hatched after 168 h (7 days). Newly hatched larvae were used for the yolk-sac larval experiment (7.2–9.0 mm standard lengths). After the yolk was consumed and feeding established at 288 h (12 days) after fertilization, the post-yolk-sac larval (9.4–13.4 mm standard lengths) experiment was conducted with the remaining larvae.

In all cases water in the test containers was changed prior to benzene exposure. At the beginning of incubation, in all 3 experiments, an antibiotic treatment of 5 ppm erythromycin gluceptate was given to reduce excessive bacterial epifloral growth on the chorion. Other physical-chemical conditions in the test containers are presented in Table 1.

Post-yolk-sac larvae were fed the marine rotifer, *Brachionus plicatilis*. Rotifers were reared according to methods of Theilacker and McMaster (1971) except that *Nephroselmis* sp., a small green flagellate, was used for rotifer food. We estimated the feeding rate of the larvae by measuring the decline in rotifer concentrations (Coulter Counter, Model ZBI) in the test containers and adjusted them according to fluctuations in a control rotifer population held in a similar container without larvae.

All exposures to benzene were single doses under static conditions. Benzene was introduced in the form of precalculated amounts of benzene-saturated seawater. We attempted to expose the herring to two chronic concentrations of approximately 1.0 and 0.1 μl/liter, subsequently referred to as "high" and "low," respectively. Exposed larvae were contrasted to controls; that is, embryos or larvae held under similar conditions except for the absence of benzene. The actual amount of benzene in the water varied,

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service.

TABLE 2.—*Dependent variables in benzene toxicity experiments with Pacific herring.*

		Yolk volume, dry weight, growth and development		Oxygen consumption			Caloric content		
Experiment	Stage	Sampling frequency	Sample size individuals/ treatment	Ages when tested (hours after fertilization)	Duration of test (hours)	Number of replicates/ treatment	Sampling frequency	Number of individuals per sample	Number of samples/ treatment
1	Egg	Daily	5	48, 72, 96, 120, 144	24	5	Daily	20	3
2	Yolk-sac	Daily	5	168, 192, 216, 240	24	5	Daily	3	3
3	Post-yolk-sac	Daily	5	312, 360, 456	24	5	Daily	3	3

however, due mostly to its volatile nature. Concentrations were determined on a Tracor MT 220 gas chromatograph (GC); water samples were taken immediately after the benzene-water mixture was added. The mean initial concentrations are presented in Table 1 and were 0.04 to 0.14 (low) and 0.52 to 2.10 μl/liter (high). Measurements of benzene in our 8-liter test containers have shown that the benzene concentration declines exponentially to an average of 25 to 30% of the initial concentration (Struhsaker et al. 1974) by the end of 24 h and is below the detectable level of our method (0.01 μl/liter) after 48 h.

Dependent variables measured in these experiments are outlined in Table 2 along with the sampling frequencies, sample sizes, and replicates per treatment. Yolk volumes (V) were calculated by making length (L) and height (H) measurements of the ovoid yolk sacs with an ocular micrometer and using the ellipsoid volume formula, $V = (\pi LH^2)/6$. In the dry weight determinations, samples were rinsed in distilled water, dried 24 h at 66 C and weighed on a Cahn electrobalance to ±0.1 μg. Since the egg chorions comprise over 30% of the dry weight of Atlantic herring eggs (Blaxter and Hempel 1966) and our estimates for six samples of 25 Pacific herring eggs each amounted to 29%, we subtracted the

TABLE 3.—*Descriptive equations of yolk calories, tissue calories, and catabolic calories in Pacific herring embryos and yolk-sac larvae exposed to 0 (control), low, and high concentrations of benzene. Y is calories; X is days post-fertilization.*[a]

Stage	Benzene concentrations	Equation	Curve type	r
		Yolk Calories		
Embryo (days 1–7)	Control	$Y = 1.473\,e^{0.16263X}$	Exponential	0.96
	Low	$Y = 1.484\,e^{0.17273X}$	Exponential	0.96
	High	$Y = 1.506\,X^{0.61948X}$	Power	0.94
Yolk-sac larvae (days 7–12)	Control	$Y = 0.879 - 0.0642X$	Linear	0.97
	Low	$Y = 0.865 - 0.0652X$	Linear	0.97
	High	$Y = 0.954 - 0.0725X$	Linear	0.99
		Tissue Calories		
Embryo	Control	$Y = 0.742 + (-0.8095/X)$	Hyperbolic	0.98
	Low	$Y = -0.077 + 0.0865X$	Linear	0.94
	High	$Y = -0.118 + 0.1034X$	Linear	0.91
Yolk-sac larvae	Control	$Y = 1/(2.351 - 0.0350X)$	Hyperbolic	0.29
	Low	$Y = 0.0822 + 0.0420X$	Linear	0.88
	High	$Y = 0.1484 + 0.0350X$	Linear	0.93
		Catabolic Calories		
Embryo	Control	$Y = -0.0039 + 0.0137X$	Linear	0.51
	Low	$Y = 0.1150 - 0.0118X$	Linear	0.40
	High	$Y = 0.0801 - 0.00564X$	Linear	0.22
Yolk-sac larvae	Control	$Y = -0.2516 + (3.679/X)$	Hyperbolic	0.72
	Low	$Y = -0.4326 + (5.367/X)$	Hyperbolic	0.89
	High	$Y = -0.7706 + (9.512/X)$	Hyperbolic	0.79

[a] These best-fit equations are one day out of phase with the graphs of Figure 2. The equations were calculated for the end of each 24-h period, and the graphs were calculated for the beginning of each period.

chorion weights from the total egg weights throughout the study.

Oxygen consumption as a measure of catabolism was determined with a Gilson differential respirometer. Either 25 eggs or 10 larvae were placed in each 25-ml vial with 10 ml of fresh filtered seawater, 24 h after their exposure to benzene. Five replicate vials per treatment were run for 24 continuous h and consumption values averaged over that period. After each 24-h measurement a new experiment was begun as soon as the respirometer could be refilled with new test animals and fresh seawater.

Yolk, tissue, and rotifer caloric contents were determined my means of a Parr adiabatic microbomb calorimeter. Measurements of three replicate samples per treatment were made daily (Table 2).

Energy budgets of the embryo and yolk-sac larvae were computed by the dry weight method, explained in detail by Laurence (1969). The percent decrease in yolk volume was multiplied by the original yolk weight, and this value was multiplied by the caloric value per gram dry weight of original yolk to obtain the caloric value per unit weight of yolk. Tissue weight was calculated by subtraction of yolk weight from the daily total weight of the embryo (or larva) and yolk complex. Then, the product of tissue weight and tissue caloric value per unit weight (i.e., 6,034 cal/g) yielded calories involved in anabolism.

Constructing an energy budget for feeding larvae involved determining the amount of rotifers consumed, estimating the calories ingested, and comparing this value with the tissue growth (in weight). Catabolism was estimated through the difference in tissue formed minus food ingested.

Data were analyzed by analysis of covariance, using the University of California Biomedical programs, BMD 1R (Dixon 1971) and methods of Snedecor and Cochran (1968).

RESULTS

Energy Utilization in Unexposed, Control Embryos and Larvae

Energy utilization of embryos and larvae reared under experimental conditions, with no exposure to benzene are described here. The average herring egg weighed 216 μg and contained 1.3 calories, prior to fertilization. The caloric content per unit of dry weight averaged 6,020 cal/g. For comparison, Lasker (1962) found an average of 5,386 cal/g in unfertilized sardine eggs, and Paffenhöfer and Rosenthal (1968) estimated 6,585 cal/g in Atlantic herring (yolk only).

TABLE 4.—*Calories consumed in food and tissue calories of feeding Pacific herring.*

Age	Food energy (cal) per larva			Larval tissue energy (cal) per larva		
Days	Control	Low concentration	High concentration	Control	Low concentration	High concentration
12–14	0.73	1.38	1.53	0.71	0.79	0.77
14–16	0.49	1.01	1.23	0.66	0.75	0.75
16–18	2.67	1.39	1.67	0.88	0.80	0.85
18–20	0.50	0.61	0.56	1.04	1.65	0.78
20–22	1.78	0.45	1.45	1.11	1.60	1.08
Totals	6.17	4.84	6.44	4.40	5.59	4.23

During incubation the energy available to developing embryos (yolk weight and yolk calories) declined exponentially to about 30% of the original amount (Figs. 1A, 2; Table 3). After hatching, 7 days (168 h) after fertilization, larvae continued yolk consumption linearly to completion of yolk absorption on day 12 (Figs. 1A, 2; Table 3).

Anabolic energy in terms of embryo tissue weight (tissue calories followed a similar trend) increased hyperbolically to day 5, then decreased just prior to hatching (Fig. 1B, Table 3). From day 6 to hatching on day 7, weight again increased. After hatching, larval tissue weight declined until day 9, then gradually increased linearly until feeding on day 12 (Fig. 1B, Table 3). After initiation of feeding, tissue weight increased more rapidly (Fig. 1B, Table 4).

Catabolic energy (difference between yolk or food calories used and tissue calories formed) was highly variable. Catabolic calories in embryos were low until day 2, then increased on day 3 to almost 0.2 calories (Fig. 2). They then varied daily with no significant discernible pattern through hatching until energy in the yolk was essentially depleted on day 12. No energy deficit (catabolic calories exceeding anabolic calories) occurred through the period of en-

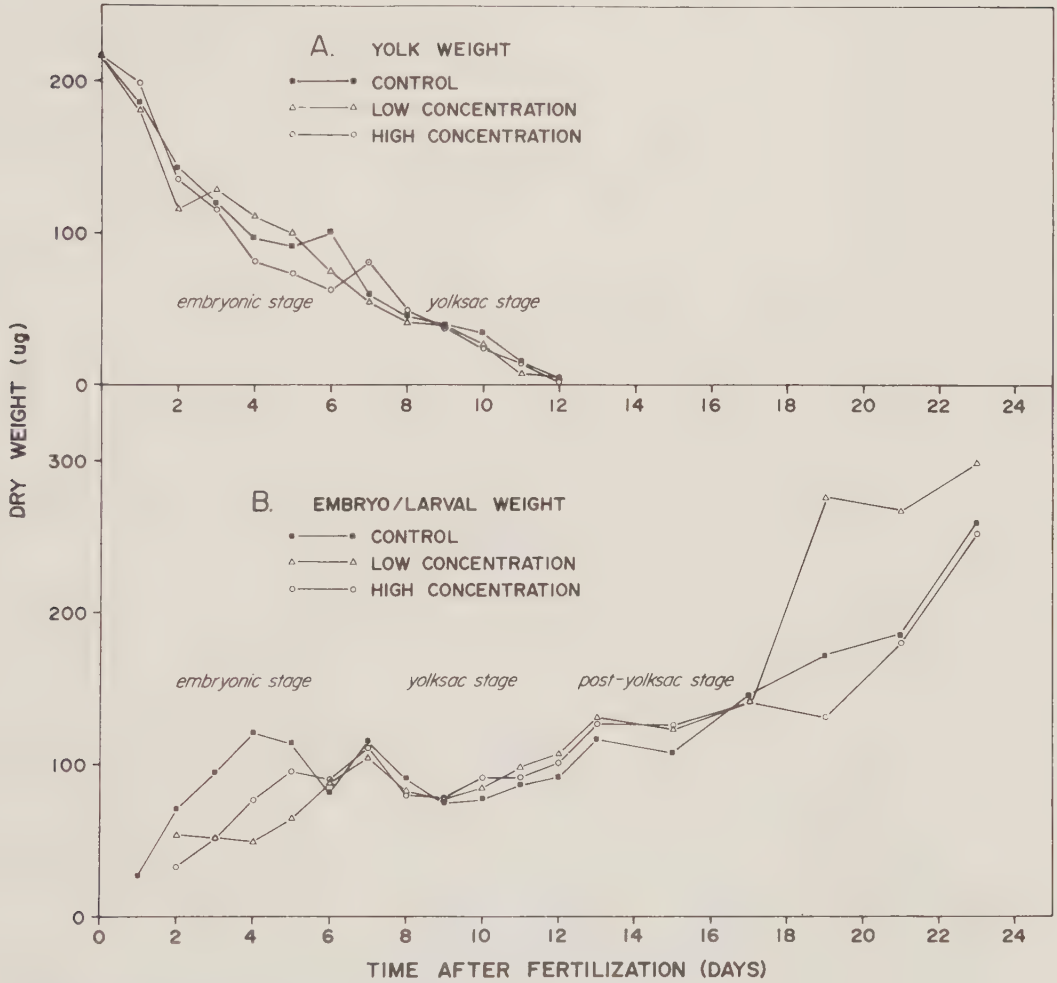

FIGURE 1.—*Dry weights (μg) of yolk (A) and embryonic and larval tissues (B) from Pacific herring exposed to high, low, and zero (control) benzene concentrations.*

dogenous energy utilization in control embryos and larvae.

Embryonic metabolic rates estimated from measurement of oxygen consumption showed a rapid prehatch increase on day 6, then declined (Fig. 3). After hatching on day 7, larval metabolism increased rapidly by approximately tenfold. Another decline occurred on day 10 prior to feeding; then consumption gradually increased through yolk absorption on day 12 into feeding (day 12 to end of experiment on day 21).

Feeding began on day 12 (288 h). Trends in calories of food energy consumed were less definable than those of endogenous yolk energy consumed, primarily due to the highly variable grazing rate of larvae (Table 4). The larvae were provided rotifers at an initial concentration of 14–20 rotifers/ml, a density found adequate for *Engraulis mordax* larvae (Theilacker and McMaster 1971). The caloric value of the rotifers was established by bomb calorimetry to be 11.6×10^{-4} cal/rotifer; an average of three samples (mean dry weight = 0.905 μg). This value was slightly higher than that of Theilacker and McMaster's (1971) value of 8.0×10^{-4} cal/rotifer, the difference possibly due to the greater weights of our egg-bearing adult rotifers. The herring larvae grazed nearly all the rotifers within 24 h. When we increased the density to over 20 rotifers/ml

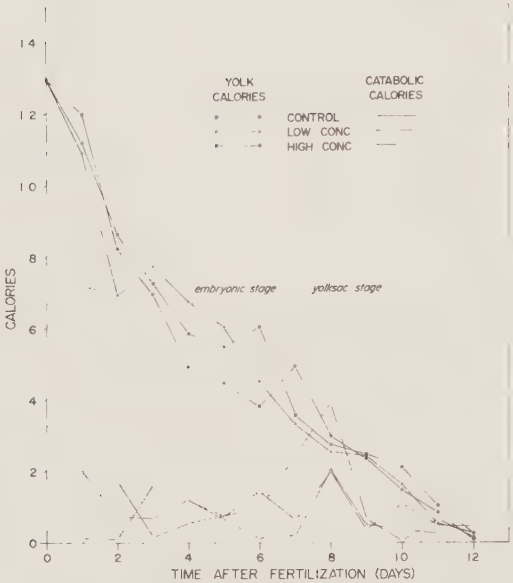

FIGURE 2.—*Catabolic and yolk calories of Pacific herring embryos and yolk-sac larvae exposed to high, low, and zero (control) benzene concentrations.*

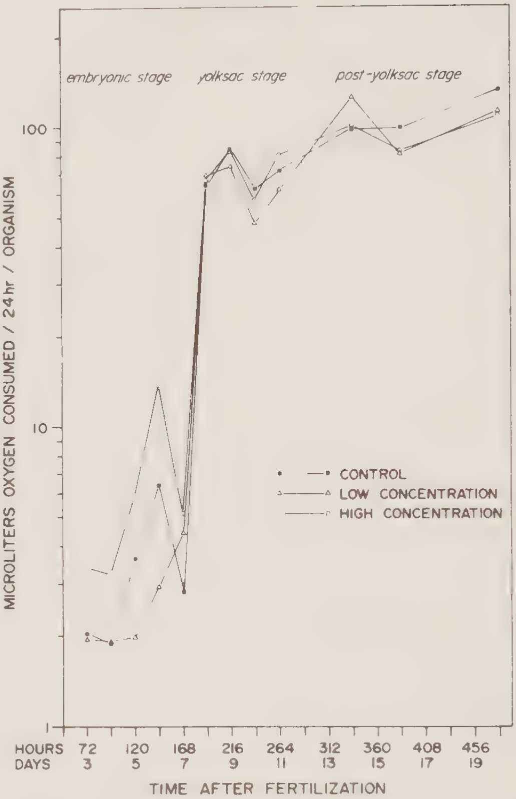

FIGURE 3.—*Oxygen consumption of Pacific herring embryos, yolk-sac larvae and post-yolk-sac larvae exposed to high, low and zero (control) benzene concentrations.*

on day 16, they still ate all that was available up to a maximum of 45 rotifers/ml in one container. This indicates that the satiation level may never have been reached during the experimental period. The estimates of energy intake were calculated directly from numbers consumed per larva per unit time. These estimates, however, may be biased because no corrections for assimilation and digestive efficiency were included.

Feeding larvae grew steadily and appeared to increase their assimilation rates near the end of the experiment (Fig. 1B, Table 4). Metabolic rates also were increasing (Fig. 3) as indicated by respiration, a result of, among other things, increased size and activity.

Effects of Benzene on Energy Utilization in Embryos and Larvae

The effects of exposure to benzene on energy utilization were determined by contrasting exposed with control embryos and larvae. Relatively low sublethal concentrations of benzene were chosen in an attempt to approximate field concentrations and to test for limiting or controlling effects on energy utilization in sensitive stages of embryos and larvae. No mortality occurred over the experimental period. However, some significant effects were found on embryonic and post-yolk-sac larval growth and oxygen consumption.

During incubation, days 1 to 7, it appeared that embryos exposed to the higher concentration of benzene consumed yolk (weight and calories) more rapidly than controls (Fig. 1A, 2; Table 3). The difference, however, was not significant when tested. No significant differences in yolk consumption occurred between exposed and control yolk-sac larvae.

Anabolism in embryos exposed to both low and high concentrations increased linearly from days 1 to 6 (Fig. 1B, Table 3). However, tissue weights of exposed embryos were significantly less than in controls. Both high and low concentrations caused significantly delayed growth (Table

TABLE 5.—*Analysis of covariance comparing tissue dry weights of Pacific herring embryos and post-yolk-sac larvae exposed to 0, 1.0, and 0.1 µl/liter benzene.*

						Deviation from regression		
Stage	Treatment	df	Σx^2	Σxy	Σy^2	df	Sums of squares	Mean square
Embryo	Control	7	0.420	61.975	13,608.709	6	4,463.707	743.951
	Low concentration	7	0.420	60.250	9,705.680	6	1,062.674	177.112
	High concentration	7	0.420	71.965	12,966.329	6	635.469	105.911
						18	6,161.850	342.325
	Pooled, W	21	1.260	194.190	12,966.329	20	6,352.340	317.617
	Difference between slopes					2	190.490	95.245
	Between, B	2	0.000	0.000	3,048.468			
	W & B	23	1.260	194.190	39,329.185	22	9,400.807	427.309
	Between adjusted means					2	3,048.467	1,524.234
	Comparison of slopes:	$F = 95.245/342.325 = 0.278$(df = 2,18); $P > 0.05$						
	Comparison of elevations:	$F = 1{,}524.234/317.617 = 4.780$(df = 2,20); $P \leq 0.05$						
Post-yolk-sac	Control	5	0.700	95.820	15,026.000	4	1,909.611	477.403
	Low concentration	5	0.700	140.710	33,951.495	4	5,666.770	1,416.694
	High concentration	5	0.700	78.240	12,459.973	4	3,714.977	928.744
						12	11,291.358	940.947
	Pooled, W	15	2.100	314.770	61,437.468	14	14,256.443	1,018.317
	Difference between slopes					2	2,965.085	1,482.543
	Between, B	2	0.000	0.000	7,905.788			
	W & B	17	2.100	314.770	69,343.256	16	22,162.231	1,385.139
	Between adjusted means					2	7,905.788	3,952.894
	Comparison of slopes:	$F = 1{,}482.543/940.947 = 1.576$(df = 2,12); $P \geq 0.05$						
	Comparison of elevations:	$F = 3{,}952.894/1{,}018.317 = 3.882$(df = 2,14); $P \leq 0.05$						

5). By hatching, 7 days after the initial exposure, the anabolic differences between exposed and control embryos were insignificant. As in yolk consumption, there were no significant differences in tissue weight and growth between exposed and control yolk-sac larvae. The effects of benzene exposure (at these concentrations) would appear to be minimal at this stage after hatching.

Feeding post-yolk-sac larvae were exposed to benzene on day 13. Until day 17 exposed larvae ingested more food than unexposed larvae (Table 4). Corresponding tissue weights of exposed larvae were heavier during that period but not significantly different. However, after day 18, larvae exposed to low benzene concentration demonstrated much higher growth and assimilation which proved to be significant (Fig. 1B, Table 5).

Catabolic calories were as variable in exposed embryos and larvae as in controls (Fig. 2). No significant differences between exposed and control embryos and yolk-sac larvae occurred except on day 8, when yolk-sac larvae exposed to the higher concentration showed higher catabolism, at that time exceeding anabolism, and an energy deficit.

Embryos exposed to benzene also showed significant differences in oxygen consumption from day 1 to hatching (Fig. 3; Table 6). High benzene concentration caused greater oxygen consumption while low concentration caused depressed consumption relative to controls. Differences at later larval stages were not significant, except toward the end of the experiment when control post-yolk-sac larvae appeared to respire more rapidly than exposed larvae.

DISCUSSION

The amount of endogenous energy available to Pacific herring embryos and larvae differed considerably from their Atlantic counterparts. Paffenhöfer and Rosenthal (1968) found the smaller Atlantic herring

TABLE 6.—*Analysis of covariance comparing oxygen consumption of Pacific herring embryos (days 1–7).*

					Deviation from regression		
Treatment	df	$\sum x^2$	$\sum xy$	$\sum y^2$	df	Sums of squares	Mean square
Control	20	3.412	3.856	152.536	19	148.178	7.799
Low concentration	24	4.262	9.281	49.018	23	28.810	1.253
High concentration	24	4.262	15.849	620.106	23	561.173	24.399
					65	738.161	11.356
Pooled, W	68	11.937	28.980	821.659	67	751.273	11.213
Difference between slopes					2	13.112	6.556
Between, B	2	0.009	−0.980	180.98			
W & B	70	11.946	28.006	1,002.639	69	936.982	
Between adjusted means					2	185.709	92.855
Comparison of slopes:	F	6.556 11.356 – 0.577(df = 2,65); $P > 0.05$					
Comparison of elevations:	F	92.855 11.213 – 8.281(df = 2,67); $P \leq 0.01$					

(216 vs. 170 μg) to contain 0.748 calories vs. 1.298 calories for Pacific herring. The magnitude of the difference may change since egg size was found to vary by a factor of 1.5 within the same female (Blaxter and Hempel 1963). The amount contained in other marine species indicates a very wide range of values with Pacific herring tending towards the upper end of the range. Cooney's (1973) study of three tropical Hawaiian species showed *Caranx mate* to have 1.131, *Etrumeus micropus* 1.007, and *Abudefduf abdominalis* 0.344 cal/egg. Lasker (1962) found the clupeid *Sardinops caerulea* to have only 0.300 cal/egg. Freshwater fishes also show wide variability. *Lepomis macrochirus* had 0.924, according to Toetz (1966), while *Micropterus salmoides* had 2.284 cal/egg (Laurence 1969).

Developing embryos consumed yolk in a linear fashion, and despite the greater metabolic rate demonstrated by the prehatch rise in oxygen consumption no energy deficit was seen. The prehatch rise in oxygen consumption has been observed in Atlantic herring (Holliday et al. 1964) and is mostly attributable to embryonic activity associated with hatching.

The order of magnitude increase in yolk-sac larval metabolism over embryonic metabolism (Fig. 3) is best explained by increased activity since the respiring biomass of the about-to-hatch embryos and the newly hatched larvae are not so dissimilar as to account for the difference in oxygen consumption. The metabolism measured by the Gilson differential respirometer was "routine" metabolism, defined by Fry (1971) to be the rate influenced by random activity under experimental conditions. The restrictive confines of the 25 ml respiratory flasks appear to have increased larval activity. Holliday et al. (1964) and Lasker (1962) demonstrated that activity was the most influential factor affecting oxygen uptake in both embryos and larvae. Active Q_{O_2}s exceeded resting values by as much as 5 to 10 times.

Significant effects of benzene on herring eggs and larvae were confined to anabolism and oxygen consumption. The suppressed embryonic growth, increased growth of post-yolk-sac larvae, and divergent oxygen consumption rates reflected alterations in the metabolic rate, yolk energy being diverted from assimilation to detoxification of benzene and/or its metabolites. Both increased and decreased metabolic rates were seen in juvenile chinook salmon and striped bass exposed to benzene (Brocksen and Bailey 1973). Other oil compounds also have affected embryonic metabolism. Lindén (1974, 1976) found oil dispersants and dispersant and oil mixtures slowed heartbeat rates in Baltic herring (*Clupea harengus*), indicating reduced metabolism.

By increasing growth in feeding larvae low benzene concentration appears to have a beneficial effect. We have also seen cases where low concentrations of both benzene and xylene caused higher hatching percentages in herring. This phenomenon has been

TABLE 7.—*Percent yolk utilization efficiency of ten species of fish.*

Species	% efficiency	State of development	Reference
Micropterus salmoides	35.2	To hatching	Laurence (1969)
Salmo salar	41.0	To hatching	Hollett and Hayes (1946)
Clupea harengus	67.8	To hatching	Paffenhöfer and Rosenthal (1968)
Clupea harengus	50.0 to 74.0	To hatching	Blaxter and Hempel (1966)
Clupea pallasi	74.4	To hatching	Eldridge et al. (this study)
Clupea pallasi	43.9	To yolk absorption	Eldridge et al. (this study)
Micropterus salmoides	44.4	To yolk absorption	Laurence (1969)
Salmo fario	56.0	To yolk absorption	Gray (1928)
Etrumeus micropus	57.9	To yolk absorption	Cooney (1973)
Salmo gairdneri	60.2	To yolk absorption	Smith (1957)
Caranx mate	75.1	To yolk absorption	Cooney (1973)
Abudefduf abdominalis	75.3	To yolk absorption	Cooney (1973)
Sardinops caerulea	77.0 to 79.0	To yolk absorption	Lasker (1962)

noted in many toxicological experiments wherein animals receiving small doses appeared healthier than controls. Smyth (1967) proposed an explanation in the form of "sufficient challenge." Small chronic doses of a toxicant exercise adaptive physiological functions which serve in healthy organisms to maintain homeostasis. In some instances this adaptive response can be measured in a positive mode, resulting in an apparent benefit to the test organism.

Yolk utilization efficiencies of controls declined when incubation period is compared to the entire yolk-sac period (Table 7). This agrees with dry weight and metabolic measurements in that larval activity and its high metabolic demand resulted in conversion efficiencies lower than in embryos. This pattern also coincides with Blaxter and Hempel's (1966) Atlantic herring observations. In comparison to developmental efficiencies in other fishes, our results tend toward the high end during incubation and the low end through yolk absorption (Table 7). At least during incubation unexposed Pacific herring were slightly more efficient than Atlantic herring.

If one considers the early life forms as "the expression of a pattern of processes of an ordered system of forces" (Von Bertalanffy 1950), it is necessary to understand the factors controlling, directing, masking, and otherwise affecting these dynamic systems. Hjort (1926) has hypothesized that year-class strength is largely determined by mortality in the early developmental stages. It therefore follows that any potential pollutant which can be shown to affect this dynamic system has implications for the organism's survival and ultimately its population. We have found that benzene in low concentrations can modify the metabolic processes of Pacific herring embryos and larvae. It remains to be determined whether the extent of the effect is sufficient to disrupt fatally the internal "ordered system."

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7. TUNA/ENVIRONMENT PROGRAMMES AT THE SOUTHWEST FISHERIES CENTER, LA JOLLA, Ca., U.S.A.

by

R.H. Evans

7.1 Introduction

Scientists of the Southwest Fisheries Center (SWFC), the Inter-American Tropical Tuna Commission and others have for a number of years studied the effects of the marine environment on the distribution, abundance and availability of tropical and temperate tunas. Much of this work has been essentially descriptive. For example, compilations of catch statistics and the results of tagging experiments have been used to define distribution limits and migration patterns (Schaefer et. al., 1961; Fink and Bayliff, 1970), and atmospheric and oceanic climatology has been used to describe the current structure and water mass characteristics within these limits (Sette, 1955, Owen, 1968). Also, environmental variables such as wind speed, sea surface temperature, mixed layer depth, water colour and dissolved oxygen content have been used as indicators of distribution and availability (Laevastu and Rosa, 1963; Blackburn, 1963; Green, 1967).

These studies have done much to describe the tuna's habitat and behaviour. Further, they have led us closer to the solutions of problems which are of paramount importance in understanding how the environment affects the availability and exploitation of tunas. These problems include:

(i) The complex manner in which atmospheric, oceanic and biological processes interact to affect survival during the larval stages.

(ii) The feedback mechanisms through which these same atmospheric, oceanic and biological processes are modulated in both space and time.

(iii) The manner in which fluctuations of the marine environment, as well as economic and political factors tend to affect the distribution of fishing effort and consequently the size of the resulting harvest.

These problems are the subject of continuing research at the SWFC where recent studies have established the need for a detailed time series of environmental data from the fishing grounds.

Traditionally, environmental data for fisheries research have been collected from cruises aboard research vessels. More recently these same data have been acquired from merchant ships and ships of opportunity. The latter has proved to be the more economical approach, but incoming data still tend to be sporadic in both areal and temporal coverage. SWFC researchers have moved to alleviate this problem by supplementing these traditional sources of environmental data with satellite data and data collected by tuna fishermen on the fishing grounds.

7.2 Background

Fisheries environment related studies at the La Jolla Laboratory take a number of forms but three ongoing programmes stand out because of their cooperative involvement with fishermen and the real-time nature of the data exchanged by the participants. The first programme, the publication of Fishing Information, utilizes "real-time" marine weather observations to create contoured charts of selected environmental variables which are averaged over periods of 15 days and a month. These analyses, together with summary tests are then printed and mailed to fishermen and other interested parties. The second programme, Chart 3 - One degree Celsius contours[1] of mean sea surface temperature for the month from the eastern North Pacific (see Fig. 2). The areal coverage of this analysis: 18°-60°N and 113°-180°W. Mean values of sea surface temperature for selected shore stations along the west coast of North America as well as ocean station "Papa" (5°N and 145°W) are also included.

Chart 4 - One degree Celsius contours of sea surface temperature for the month from the western North Pacific. The areal coverage of this analysis: 15°-60°N and 170°W-115°E.

Chart 5 - Deviation of the sea surface temperature in the eastern North Pacific for the month from the long-term mean 1948-67. Areal coverage of this analysis is identical to Chart 3. The deviation from the long-term mean is contoured at ± 1 degree Celsius intervals.

Chart 6 - Deviation of the sea surface temperature in the western North Pacific for the month from the long-term mean 1948-67. Areal coverage of this analysis is identical to Chart 4 and the contour interval is the same as Chart 5.

Chart 7 - Deviation of the sea surface temperature in the eastern North Pacific for the month from the corresponding sea surface temperature values for the same month of the previous year. The areal coverage of this analysis and the contour interval are the same as Chart 5.

Chart 8 - One degree Celsius contours of sea surface temperature for the month from the eastern tropical Pacific. Areal coverage of this analysis: 30°N-~30°S[2] and 70°-180°W.

Chart 9 - Deviation of the sea surface temperature in the eastern tropical Pacific for the month from the long-term mean 1948-67. The areal coverage of this analysis is identical to Chart 8. The deviation from the long-term mean is contoured at ± 1 degree Celsius intervals.

Chart 10 - Surface temperature, surface salinity and subsurface temperature structure obtained from expendable bathythermograph (XBT) transects taken between west coast ports in the United States and Hawaii. The data for these analyses come from 4 hourly XBT drops and surface salinity samples collected by cooperating merchant vessels along their scheduled routes. The XBT equipment aboard the vessels is provided and maintained by Pacific Environmental Group personnel stationed at Tiburon, California. The Pacific Environmental Group is a laboratory within the Southwest Fisheries Center.

Charts 11 and 12 - Expendable bathythermograph and surface salinity transects similar to the analyses described in Chart 10. These additional analyses are included in FI when more than one transect is available for the month.

Each month the text and charts that comprise FI are drafted, printed and distributed; the product reaching the subscriber near the end of the month following the analysis. The dissemination of Fishing Information is identical to that for the "supplement".

Each month about 18,000 marine weather observations are used to produce FI. These observations are also used to produce additional environmental data summaries for ongoing research projects of the SWFC and the NORPAX (North Pacific Experiment) at the Scripps Institution of Oceanography. At the end of each month the entire observational data the "Cooperative Tropical Tuna Advisory Programme", utilizes marine weather data and expendable bathythermograph (XBT) data to produce daily weather and sea state charts and weekly sea surface temperature (SST) and mixed layer depth (MLD) charts of the eastern tropical Pacific. These charts are broadcast by radio facsimile (FAX) to cooperating purse-seiners from radio station WWD, a National Marine Fisheries Service licensed radio station in La Jolla, California.

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[1] Sea surface temperatures for the FI monthly publication were changed from Fahrenheit to Celsius starting with the March 1977 issue.

[2] The southern limit of coverage is dependent each month on the amount of sea surface temperature data available in the chart area.

A third programme, the Albacore Advisory Programme, provides weekly SST charts and narrative texts of fishing conditions to albacore fishermen off the west coast of North America. The Albacore Advisory Programme is described in detail in section 8.

Both Fishing Information and the FAX Programme depend heavily on "real-time" weather observations. Internationally formatted marine weather observations are received at the SWFC from Washington, D.C. via a 100-word per minute National Weather Service (NWS) teletype circuit. Each weather observation is then converted to a computer card image suitable for computer processing. At weekly intervals these observations are computer edited to remove duplicate and erroneous observations. The resulting data files are then processed using a suite of computer programmes which create weekly, bi-weekly, and monthly summaries of selected environmental variables.

7.3 Data collection and environmental product preparation

7.3.1 Fishing information

Of the Fishery/Environment related advisory programmes at the SWFC, Fishing Information (FI) is the oldest. FI was started in 1957 at the Honolulu Laboratory of what was then the Bureau of Commercial Fisheries (BCF). Monthly charts of sea surface temperature for the North Pacific were prepared to gain a better understanding of albacore migrations. In 1960 the task of preparing these charts was transferred to the Tuna Forecasting Programme at the La Jolla Laboratory, where they were published in the California Fishery Market News Monthly Summary, Part II. At that time, the project was expanded to include the issuance of a bi-weekly SST chart as well as a monthly plot of average SST's for the eastern tropical Pacific. In ensuing years through 1974, the content of FI was altered frequently in response to user requests. In 1970 the publication was expanded to include SST charts of the western North Pacific. In addition, the 1° square plots of SST in the eastern tropical Pacific were converted to contoured charts of SST.

The current bi-weekly component of FI is a sea surface temperature chart for the eastern North Pacific covering an area from the west coast of North America westward to 136.5° W between 25° and 52° N. At 15 day intervals about 1200 SST observations, averaged by one degree squares, are contoured at two degree Fahrenheit intervals to produce the bi-weekly chart (see Fig.1). This chart, entitled "FISHING INFORMATION - supplement", is then mailed to about 725 subscribers on a "no-cost-to-the-subscriber" basis. The mailing list for the supplemental chart as well as for Fishing Information is presently limited to 750 subscribers.

The parent publication of the supplemental chart is a collection of environmental analyses. FI contains narrative descriptions of current meteorological and oceanographic conditions in the north and eastern tropical Pacific as well as 10 to 12 charts of selected environmental variables for the same areas. The content of these charts is as follows:

Chart 1 - Seventeen-year mean (1961-1977) of observed sea level values of barometric pressure, and (by 5 degree squares) the resultant wind direction, resultant wind speed and average wind speed. The areal coverage of this analysis: 20°-60°N and 115°-180°W.

Chart 2 - Observed sea level values of barometric pressure for the current month; and (by 5 degree squares) the resultant wind direction, resultant wind speed and average wind speed. The areal coverage and format of this analysis is identical to Chart 1.

set as well as certain data summaries are archived on magnetic tape and stored at the SWFC. This data set, which has been maintained since June 1960, forms a unique data source for ongoing studies of the environment and climatology of the Pacific Ocean.

7.3.2 Cooperative Tropical Tuna Advisory (FAX) Programme

By 1970 United States tuna purse-seiners were beginning to range further westward from the coast of Central America in search of yellowfin and skipjack tuna. The offshore fishing areas were outside standard shipping routes and it appeared that the purse-seiners might provide useful information from this "data sparse" region. As a result, the SWFC instituted the Cooperative Tropical Tuna Advisory Programme, designed to foster an exchange of environmental data between tropical tuna fishermen and researchers at the SWFC (Eber, 1976).

To effect this exchange of data, two fundamental problems had to be overcome. The first was how to provide useful environmental information to vessels which routinely remained at sea for periods of 3 months or more. A pilot project in the summer of 1970 demonstrated the feasibility of long range communications between the tuna vessels operating in the eastern tropical pacific and radio station WWD. The project indicated however, that the transmission of large amounts of verbal information by WWD and the assimilation of these data by the tuna seiners was difficult and time consuming.

Radio facsimile appeared to offer a viable means of transmitting the needed data to the tropical tuna fleet in "real-time". In late 1970 three facsimile units that were surplused by the U.S. Navy were obtained and modified to copy radio facsimile transmissions. These units were installed on three XBT equipped purse-seiners during the 1971 fishing season.

The second problem that had to be solved was how to allow the participating vessels to radio positional and environmental data to WWD without revealing their positions to other purse-seiners. Since the tropical tuna fishery is so competitive and covers such a large area of the eastern tropical Pacific, fishermen tend to operate independently or in small groups. The geographical location of these operating units is a closely guarded secret and is considered by many fishermen to be essential to the success of the fishing operation. To allow the cooperating fishermen to keep their position secret it was necessary to devise a coding system for them to use in reporting the position of their observations. This was done by providing each participant with his own unique location code. The use of this code has allowed each vessel to radio XBT and marine weather data to WWD without compromising its location.

The coding scheme is administered by the U.S. Navy's Fleet Numerical Weather Central (FNWC) at Monterey, California. FNWC maintains each vessel's location code in their computer for decoding the participating vessel's geographic position. The computer programme that decodes the vessel's position outputs the data without including any vessel identification. This ensures the confidentiality of the vessel's location in all instances.

To implement this decoding scheme, environmental observations radioed to WWD by the participants are relayed to the SWFC via teletype (see Fig. 3). The observations are then transmitted to FNWC over the Navy Environmental Data Network tieline. After decoding at FNWC, the XBT and marine weather observations from the participating vessels are returned to the SWFC in decoded form. These observations are also sent via teletype from FNWC to the National Weather Service Forecast Center at Redwood City, California.

Currently WWD collects XBT and marine weather observations from the participating vessels between the hours of 2200 and 2300 GMT. These data, as well as environmental products from FNWC, the National Weather Service and APT (Automatic Picture Taking) satellite photos are utilized by the SWFC staff to create analyses for broadcast to the participating vessels. Initially, two products - the wind and weather analysis and the sea state analysis - were broadcast daily (Monday through Friday) at 2300 and 2310 GMT each day. A third chart, the weekly mean sea surface temperature analysis, was added for broadcast each Thursday at 2320 GMT (Fig. 4). A summation of all of the environmental advisories currently offered by radio station WWD is included in Table 1.

During the past six years the format and content of the FAX products offered to the participants has varied in response to user needs. A verbal advisory describing tropical storms or areas of high winds now accompanies the facsimile charts when conditions warrant. In January of 1973 a weekly mean mixed layer depth analysis (see Fig. 5) was added for broadcast at 2320 GMT each Friday. In April of 1974, the National Weather Service Forecast Center (NWSFC) in Redwood City, California became a participant in the programme by providing the wind and weather and sea state analyses for broadcast by WWD on weekends (see Fig. 3). In August of 1974 the NWSFC assumed responsibility for the preparation of these two charts. At present, the wind and weather and sea state advisories are being offered by the NWSFC through WWD twice daily, seven days a week (see Table 1).

As indicated, the services offered by the Tropical Tuna Advisory Programme have expanded dramatically since 1971. No less dramatic has been the expansion in the number of participants and the data they have provided to the SWFC. During 1971, FAX units owned and maintained by the SWFC were installed on a total of 25 purse-seiners. These participants radioed 1528 weather and XBT observations to WWD. By the end of 1975 the number of programme participants had risen to 75, who contributed 7653 environmental observations during the year. To date, more than 30,000 observations have been received, utilized and archived at the SWFC.

7.4 Programme effectiveness

An analysis of the effectiveness of the FI and FAX programmes is complicated by the fact that these are cooperative programmes that are of benefit to fishermen and researchers alike. In light of this, we must first consider the utility of the information provided to the user of environmental products, basically the fishermen. Second, we must consider the contributions to fishery-environment research that are realized from the "real-time" data and various information from the fishermen. The analysis, however, at the present time must rely on primarily qualitative rather than quantitative standards because data on a "real" value of the information to the research or fishermen have not been gathered.

Several attempts have been made by the SWFC to evaluate the utility of FI. In 1967, 1974 and 1975, surveys were conducted to characterize the subscribers and how they used the FI charts and text. In the 1975 poll, to which 548 subscribers responded, the largest single user group (33%) were commercial fishermen. Of this group, 92.1% indicated that the FI products were used in developing their fishing strategy and 77.3% indicated that the sea surface temperature charts were the most useful information contained in the publications. Of the two FI publications (monthly and bi-weekly supplement), the bi-weekly publication (see Fig. 1) was favoured over the monthly publication.

In addition to commercial fishermen, FI is also used by sport fishermen, fish processors, fisheries researchers, oceanographers, and meteorologists. Respondents in these categories indicated that the FI products were most useful in environmental and fishery research, respectively. Again the SST charts were indicated as being the most useful.

The FI programme also provides information in the form of processed data and data summaries for fisheries and marine environment research. Researchers at the SWFC, the Scripps Institution of Oceanography and elsewhere routinely use the FI data bases for monitoring long-term sea surface temperature anomalies and ocean-atmosphere heat exchang fluctuations. The FI data have also been used for locating ocean frontal boundaries and as ground truth for satellite derived SST values. In fact, the FI data base is unique in that it is the only readily available source of quasi-current information on abnormal ocean conditions, such as El Niño occurrences, for the eastern Pacific.

Attempts have also been made to evaluate the utility of the FAX programme to tropical tuna fishermen. During 1973 and 1974, 22 tuna purse-seine skippers were interviewed by SWFC staff members. Nearly all of those interviewed indicated that they copied the FAX charts daily and also listened to the verbal advisories. The fishermen indicated that the wind and weather sea state charts were of the greatest use to them. These charts allowed them to fish in the productive areas along the Inter-Tropical Convergence Zone while avoiding the tropical cyclones that frequent the area during the summer months. They also indicated that the SST and MLD charts were useful in the development of fishing strategy and day-to-day tactics.

Further information concerning the utility of the FAX charts has been obtained at annual meetings where tuna fishermen and SWFC researchers gather to discuss the FAX programme and suggest ways to improve it. These meetings, which have been held each December since 1972, provide a forum for an interchange of ideas concerning the content of the FAX advisories and the programme in general. In this way advisories of the greatest potential use to the fishermen are ensured.

In conclusion, it is impossible to state unequivocally that FI and the FAX programme are "cost effective" or have a profound influence on the cost of fish at the market place. We can only surmise from the existing information that these programmes are important to fishermen and of value to the research community.

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Table 1

Synopsis of Fishery-Environment Products Offered by the Southwest Fisheries Center through Radio Station WWD

	Type of Product	Mode of Dissemination*	Broadcast Frequency	Frequency of issue	Time of Issue (GMT)	Product Valid Time (GMT)	Areal Coverage	Product Originator	Prime User	Product Content
1.	Wind & weather analysis and forecast.	Radio facsimile	8644.1 & 17,408.6 kHz	Daily	1500 2300	0600 1800	From the west coast of N&S America to 160°W between 20°S and 37°N	National Weather Service	Tropical Tuna Fleet	Wind speed, wind direction, position of the Inter-Tropical Convergence Zone (ITCZ), cloud cover, positions of severe weather, initial and forecast positions of tropical disturbances
2.	Sea & swell analysis & forecast	Same	Same	Same	2310	1800	Same	Same	Same	Wave height, swell height, swell direction, swell period, and areas of rough seas.
3.	Weekly mean sea surface temperature analysis (tropical area)	Same	Same	Weekly on Thursday	2320	Previous 7-day period	From the west coast of N&S America to 140°W between 6°S and 30°N	Southwest Fisheries Center	Same	Weekly mean sea surface temperature (SST) isotherms derived from weekly 1° square averages of SST. Contour interval 1°C with areas of sparse data coverage indicated by dashed contours.
4.	Weekly mean mixed layer depth analysis (tropical area)	Same	Same	Weekly on Friday	2320	Same	Same	Same	Same	Weekly mean mixed layer depth (MLD) derived from energy numerical models, computed for 5° squares. The results are hand contoured at 50 foot depth intervals. Areas of sparse data are indicated by dashed contours.
5.	Tropical storm advisories	Verbal broadcasts	Same	As required	1510 2310	As indicated in broadcast	Same	Same	Same	Information concerning tropical storms or other areas of inclement weather. The broadcasts contain present and forecast positions of storms, areal extent, expected winds, direction and speed of the storm, pertinent sea state information, and other information as required.
6.	Weekly mean sea surface temperature analysis	Radio facsimile	Same	Weekly on Friday during albacore season (∿July-Oct.)	1700	Same	From the west coast of N. America to 141°W between 28° and 52°N	Same	Albacore fishermen	Weekly mean sea surface temperature (SST) isotherms derived from weekly 1° square averages of SST and hand contoured. Contoured interval 1°C.

*All broadcasts from radio station WWD are upper sideband carrier frequencies. The facsimile scan rate is 120 lines/minute with an international index of cooperation of 576.

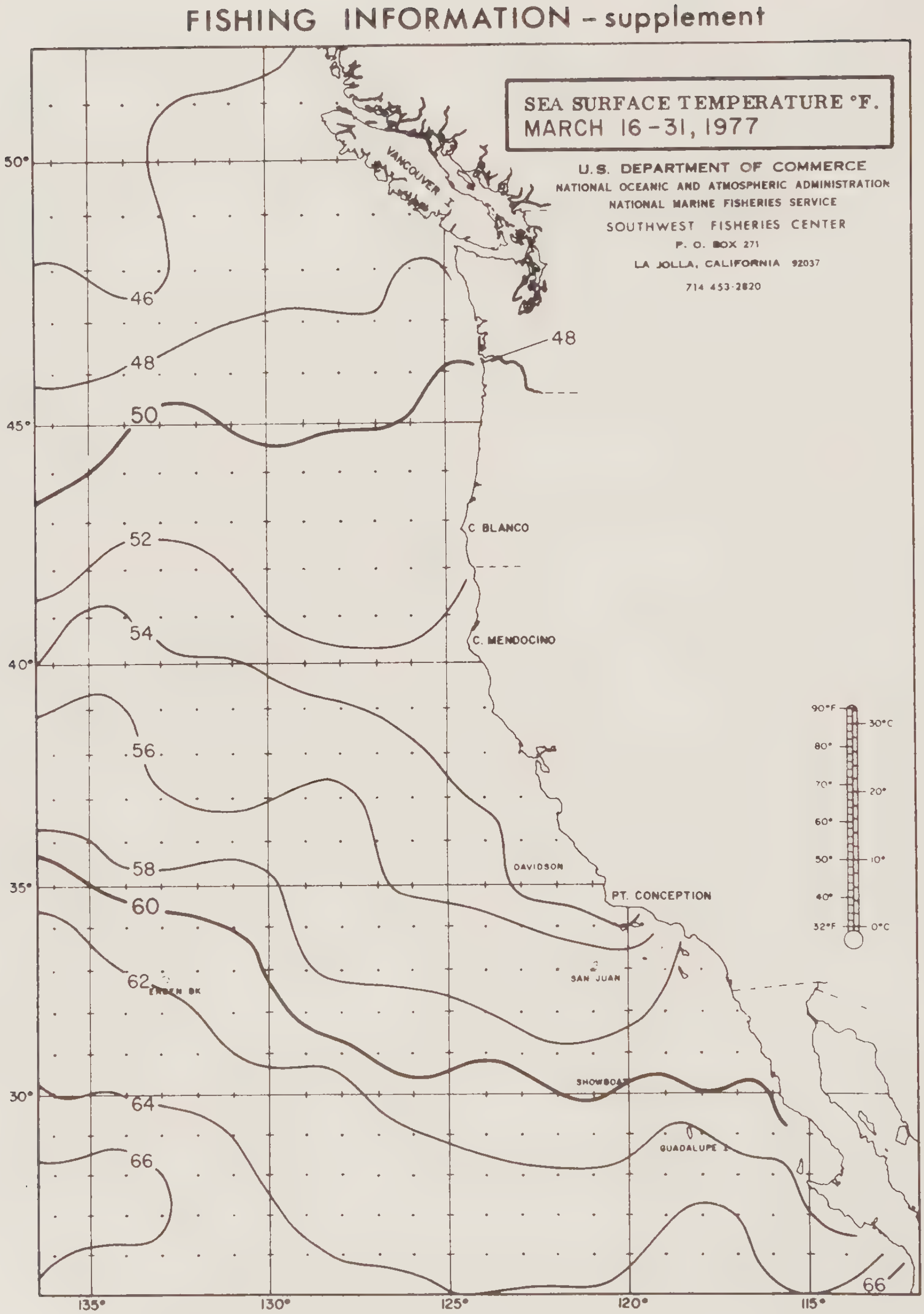
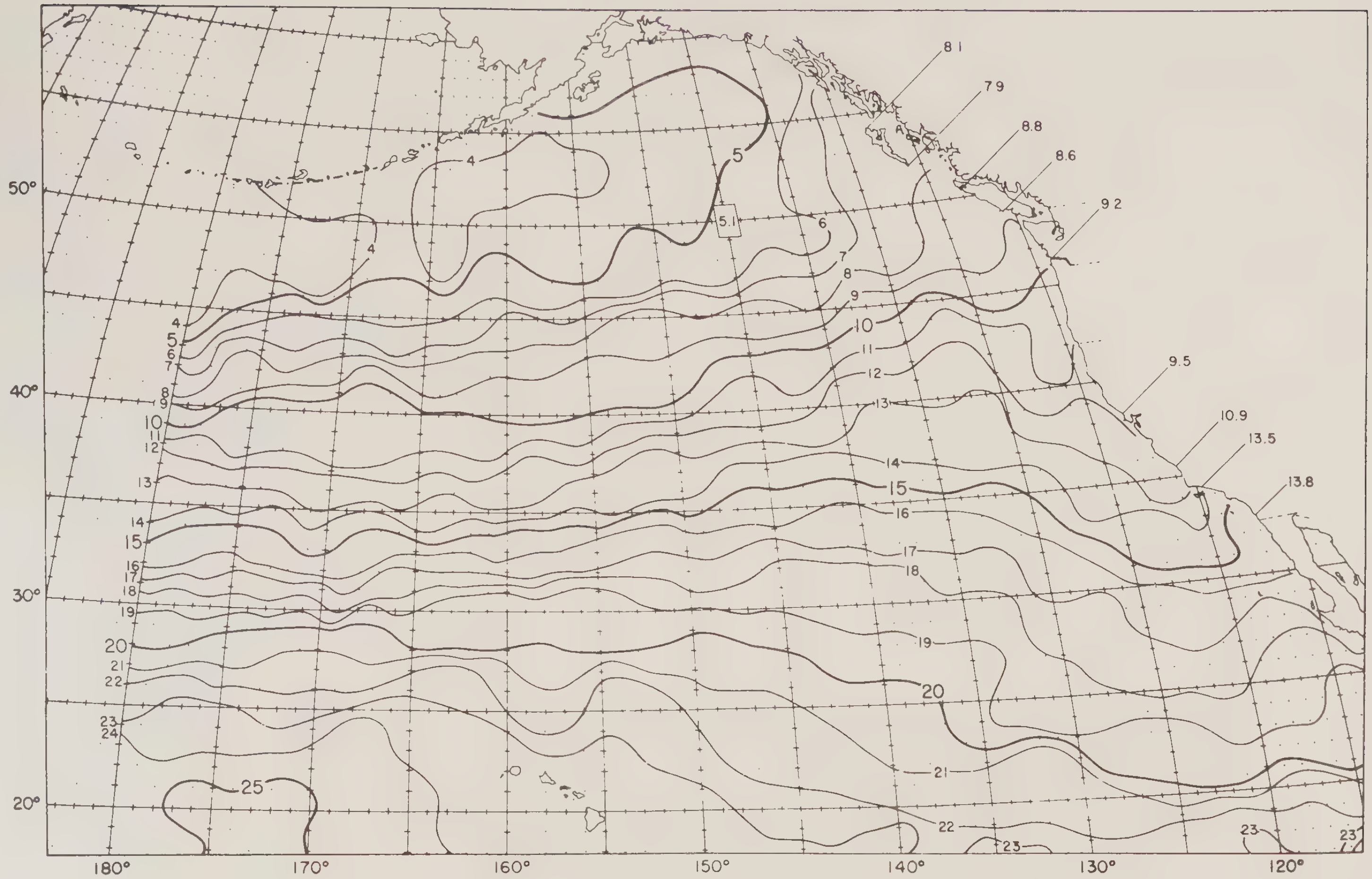

FISHING INFORMATION - supplement
SEA SURFACE TEMPERATURE °F.
MARCH 16-31, 1977
U.S. DEPARTMENT OF COMMERCE
NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
NATIONAL MARINE FISHERIES SERVICE
SOUTHWEST FISHERIES CENTER
P. O. BOX 271
LA JOLLA, CALIFORNIA 92037
714 453-2820
VANCOUVER I.
C BLANCO
C. MENDOCINO
DAVIDSON
PT. CONCEPTION
SAN JUAN
ERBEN BK
SHOWBOAT
GUADALUPE I.
46
48
48
50
52
54
56
58
60
62
64
66
66
50°
45°
40°
35°
30°
135°
130°
125°
120°
115°
90°F
80°
70°
60°
50°
40°
32°F
30°C
20°
10°
0°C

Figure 1: Example of biweekly SST chart distributed to albacore fishermen


50°
40°
30°
20°
180°
170°
160°
150°
140°
130°
120°
8 1
7 9
8.8
8.6
9 2
9.5
10.9
13.5
13.8
5.1
4
5
6
7
8
9
10
11
12
13
14
15
16
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18
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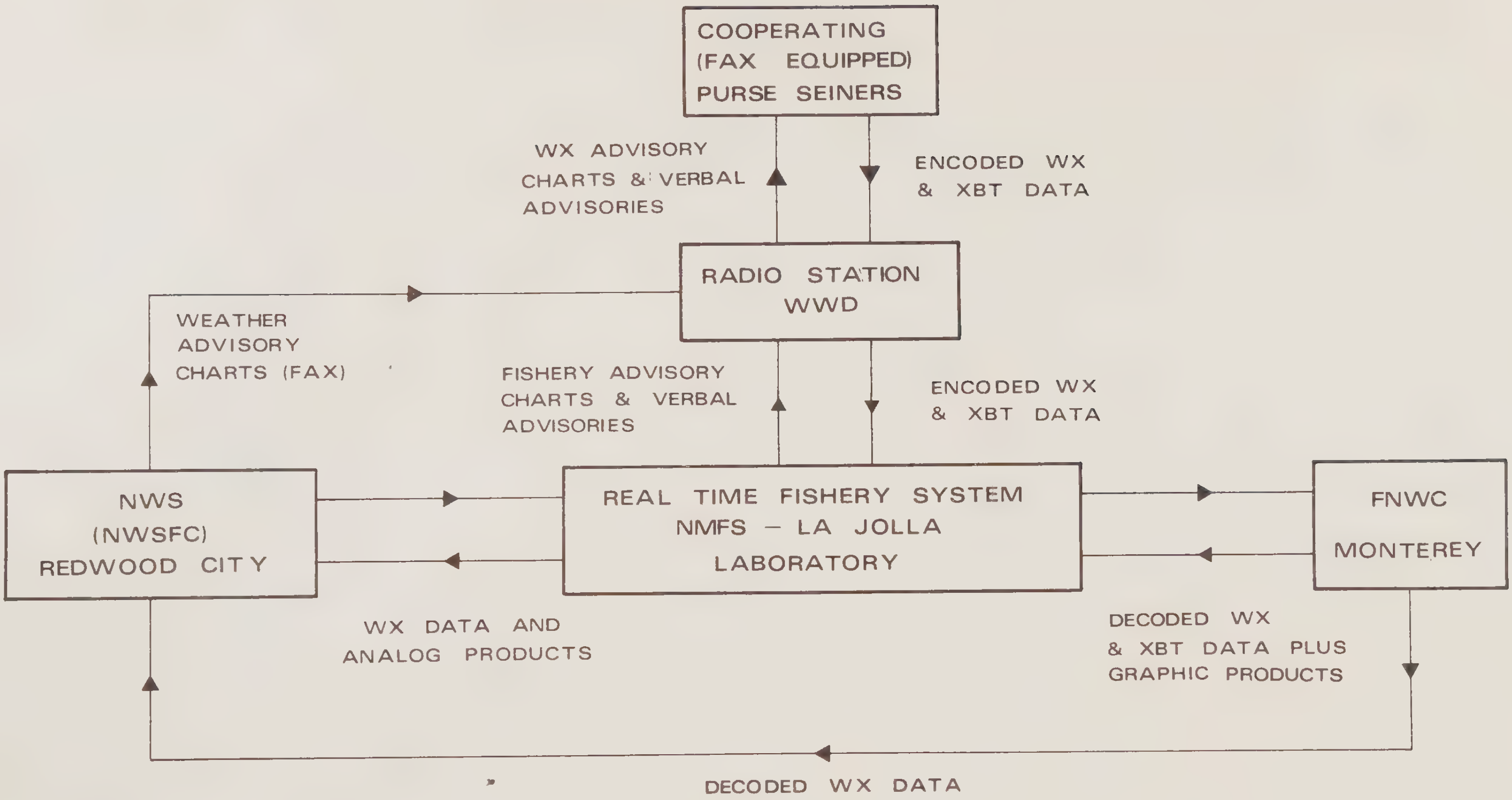
20
21
22
23
24
25

Figure 2: Example of a mean sea surface temperature map
(month of March 1977)


COOPERATING
(FAX EQUIPPED)
PURSE SEINERS
WX ADVISORY
CHARTS & VERBAL
ADVISORIES
ENCODED WX
& XBT DATA
RADIO STATION
WWD
WEATHER
ADVISORY
CHARTS (FAX)
FISHERY ADVISORY
CHARTS & VERBAL
ADVISORIES
ENCODED WX
& XBT DATA
NWS
(NWSFC)
REDWOOD CITY
REAL TIME FISHERY SYSTEM
NMFS – LA JOLLA
LABORATORY
FNWC
MONTEREY
WX DATA AND
ANALOG PRODUCTS
DECODED WX
& XBT DATA PLUS
GRAPHIC PRODUCTS
DECODED WX DATA

FAX —RADIO FACSIMILE
WX —MARINE WEATHER
XBT —EXPENDABLE BATHYTHERMOGRAPH (SURFACE & SUBSURFACE OCEAN TEMPERATURES)

Figure 3: Flow of information within the NMFS Cooperative Tropical Tuna Advisory Program

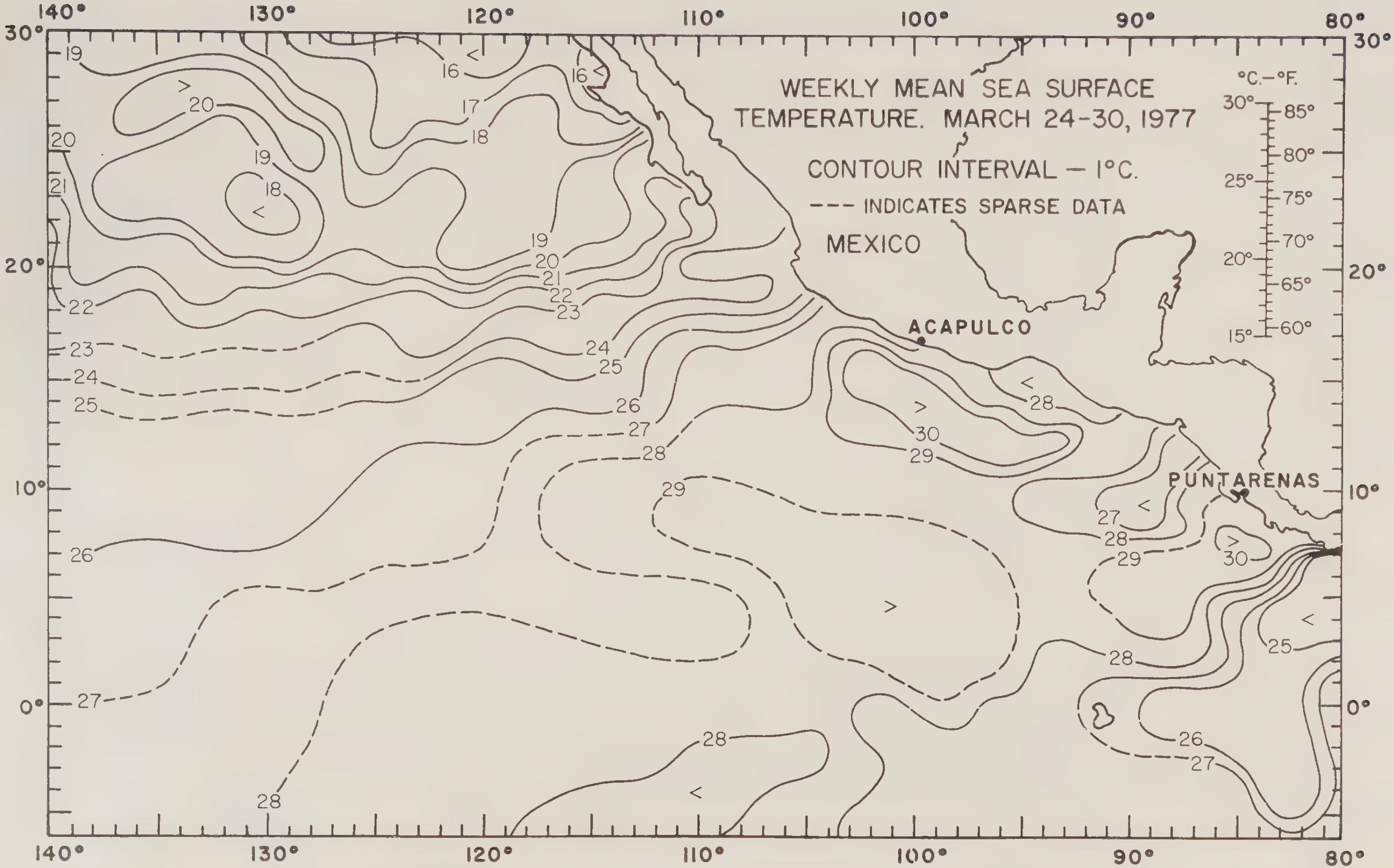

WEEKLY MEAN SEA SURFACE
TEMPERATURE. MARCH 24-30, 1977
CONTOUR INTERVAL — 1°C.
--- INDICATES SPARSE DATA
MEXICO
ACAPULCO
PUNTARENAS
°C.—°F.
30° 85°
80°
25° 75°
70°
20° 65°
15° 60°
140° 130° 120° 110° 100° 90° 80°
30° 20° 10° 0°
16 17 18 19 20 21 22 23 24 25 26 27 28 29 30

FIG. 4: U.S. DEPARTMENT OF COMMERCE, NOAA NATIONAL MARINE FISHERIES SERVICE, FOC La Jolla, Calif.

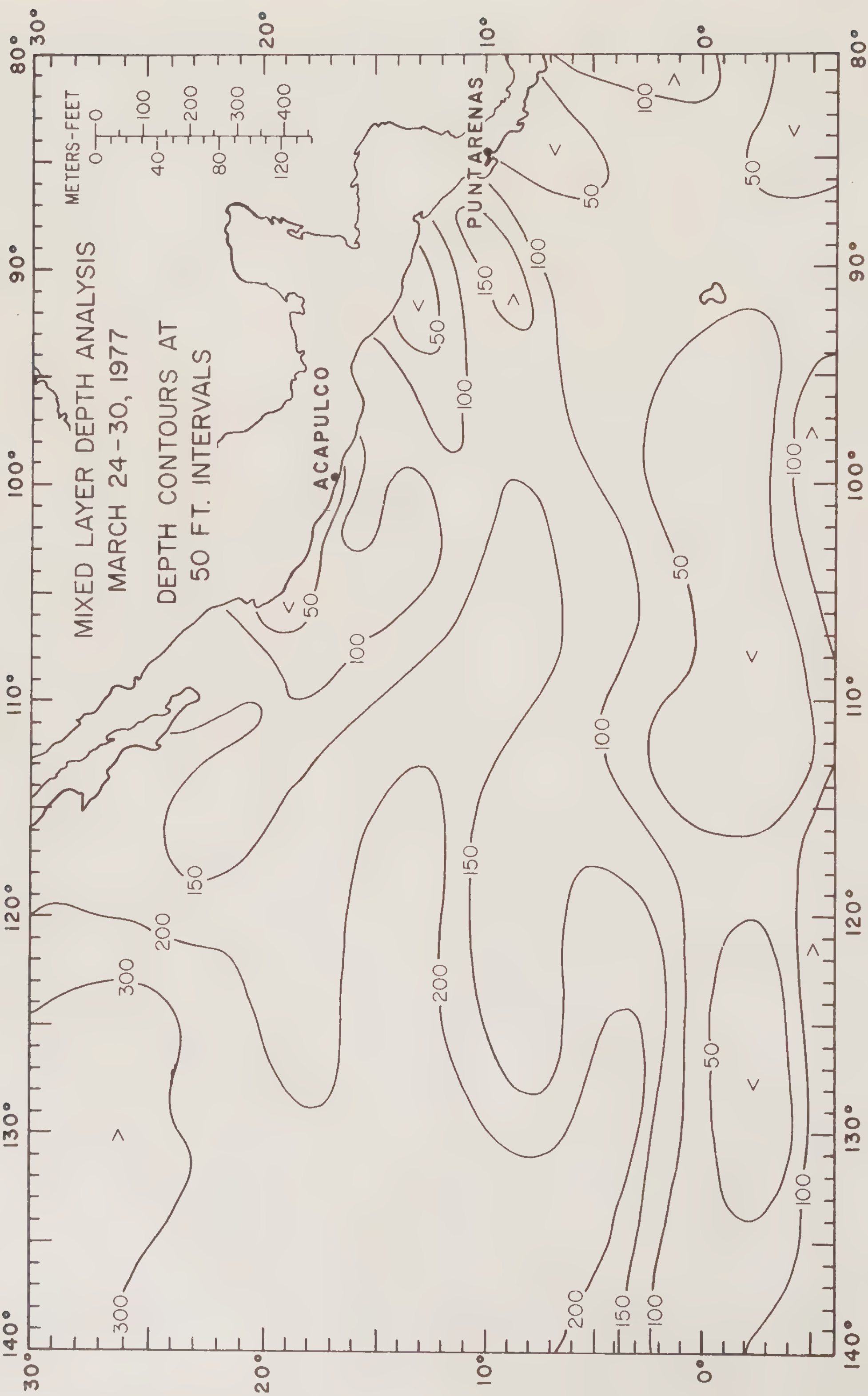

MIXED LAYER DEPTH ANALYSIS
MARCH 24-30, 1977
DEPTH CONTOURS AT
50 FT. INTERVALS
METERS-FEET
0
40
80
120
0
100
200
300
400
ACAPULCO
PUNTARENAS
50
100
150
200
300
30°
20°
10°
0°
80°
90°
100°
110°
120°
130°
140°

FIG 5: U.S. DEPARTMENT OF COMMERCE, NOAA NATIONAL MARINE FISHERIES SERVICE, FOC La Jolla, Calif.

7716

Some Effects of Stock Mixing on Management Decisions

William W. Fox, Jr.

National Marine Fisheries Service, Southwest Fisheries Center, La Jolla, California 92038

INTRODUCTION

One of the major concerns of the IWC Scientific Committee on the status and management of sperm whales has been delineating and setting quotas by unit stocks. Examining some aspects of this concern with a simple mathematical model helps to illustrate the need for careful attention to stock delineation and the degree to which two stocks are indeed independent and can be managed as such.

Lord (1971) formulated a general multiple species production model with inter-specific interaction terms and performed some mathematical analysis of the logistic form. However, there has been no attempt to apply the model to an actual fishery. Similarly, Larkin (1963) mathematically examined the competition equations of Lotka and Volterra, the logistic form, for two species in detail. The mixing of multiple stocks, however, is of specific interest to the management of sperm whales. The problem considered here is one of stocks of the same species occupying generally different, though not necessarily distinct, spaces with some degree of mixing among them. For simplicity, I will consider only two stocks and the logistic form of population production.

THE MIXING MODEL FORMULATION

Consider two logistic stocks of the same species which occupy generally different spaces, such that fishing mortality (or fishing effort) can be applied to each stock separately (F_1 and F_2), but between which there is some mixing at intrinsic rates T_1 and T_2. Consider also that these stocks are not different, other than in their origin, such that once a part of stock 1 transfers to the area of stock 2 it is indistinguishable in all aspects from stock 2 (and vice versa). The mixing model is, therefore, the set of equations:

$$\frac{dP_1}{dt} = (K_1P_1 + T_2P_2)\left(\frac{P_{max(1)} - P_1}{P_{max(1)}}\right)$$

$$-T_1P_1\left(\frac{P_{max(2)} - P_2}{P_{max(2)}}\right) - F_1P_1 \qquad 1(a)$$

$$\frac{dP_2}{dt} = (K_2P_2 + T_1P_1)\left(\frac{P_{max(2)} - P_2}{P_{max(2)}}\right)$$

$$-T_2P_2\left(\frac{P_{max(1)} - P_1}{P_{max(1)}}\right) - F_2P_2 \qquad 1(b)$$

where 1 and 2 are the designations for stocks 1 and 2.

It can be seen that the model assumes that the rates of mixing are determined by the population size in the area of origin and the amount of space available in the area of transfer – when both populations are at their carrying capacities, P_{max}, (with $F_1 = F_2 = 0$) there is no mixing. Many additional mixing models could be formulated under alternate hypotheses, but I will restrict my analysis in this document to the above equation set.

MIXING MODEL ANALYSIS

Rigorous mathematical analysis of the mixing equations could be presented (cf. Larkin, 1963; Pielou, 1969); however, it will suffice to illustrate simply a few of the implications of the model.

Fig. 1 provides the locus of equilibrium points ($dP_1/dt = 0$, $dP_2/dt = 0$) for equation set (1) – the concave upward curves for equation (1a) and concave downward curves for equation (1b) – with an arbitrary set of parameters. Additionally,

$$P_{max(1)} = 0.5\ P_{max(2)},$$

$$K_1 = K_2 = K$$

and $T_1 = T_2 = T$.

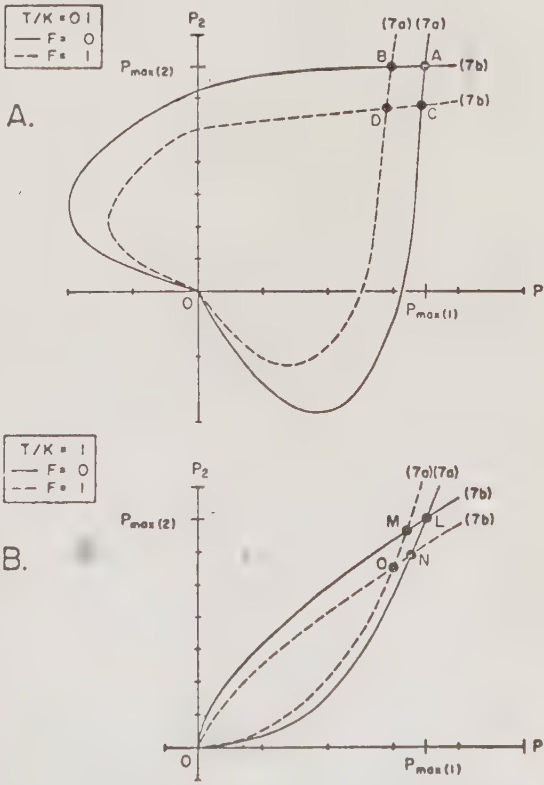


Fig. 1. Locus of equilibrium points for the production model with mixing of two species (equations 1a and 1b). (A) Low relative mixing rate; (B) High relative mixing rate.

Four combinations of fishing mortality at 0 and 1 are plotted for two cases of the mixing coefficient relative to the intrinsic rate of increase coefficient (T/K). Points of stability occur at the intersections of the concave upward and concave downward curves (heavy dots).

Fig. 1A illustrates the relationships when mixing is slow relative to population productivity, T/K = 0.1. At $F_1 = F_2 = 0$ both populations achieve their respective P_{max} (point labelled A). Applying fishing mortality to either stock has little affect on the stock not being exploited (point B or C). However, applying fishing mortality simultaneously to both stocks results in slightly lower stock sizes (point D) than exploiting just one or the other (points B and C) due to an increase in export and a loss of supporting import.

Fig. 1B illustrates the relationships when mixing is relatively high. With no fishing mortality, point L is the same as point A (Fig. 1A). An obvious difference between the low and high relative mixing rates is that the curves become more coincident as the relative rate of mixing increases, approaching a common curve as the mixing rate becomes infinite. Furthermore, the degree of synergistic lowering of both stock sizes when both are exploited (point O), as opposed to each being exploited alone (points M and N), is much greater than when the mixing rate is low (Fig. 1A).

MIXING AND THE YIELD RELATIONSHIP

The major question is: what impact does the mixing of stocks have on the shape of the yield curve? Fig. 2 illustrates the combined equilibrium yield and combined fishing effort curves (assuming catchability = 1) for four rates of mixing and three ratios of effort applications to the two stocks. All parameters are the same as in the previous section. On the vertical axes is the combined equilibrium yield from the two stocks ($Y_1 + Y_2$) and the combined fishing effort ($F_1 + F_2$) is on the horizontal axes. The dash-dot lines represent all the effort being exerted on P_1 alone, the dashed lines represent 75% of the total effort being distributed on P_1 and 25% being distributed on P_2, and the heavy lines represent an equal amount of effort being distributed on both P_1 and P_2.

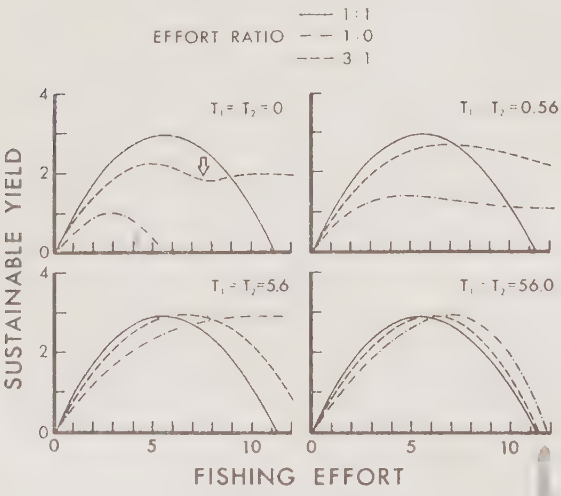


Fig. 2. Total equilibrium yield-total fishing effort curves for the production model with mixing of two species (equations 1a and 1b) at four rates of mixing.

When there is no mixing between the stocks, $T_1 = T_2 = 0$ (Fig. 2, upper left panel), obviously the total maximum sustainable yield (TMSY) increases to the sum of the MSYs of the two stocks when fished separately. Because of the nature of the parameters selected, the MSY of each stock occurs at the same F, but the MSY of P_2 is twice as large as that of P_1. Any other effort ratio produces a lower TMSY.

When the mixing rate is very large, $T_1 = T_2 = 56$ (Fig. 2, lower right panel), the model behaves as if it were one large stock, $P_1 + P_2$, as expected. The total sustainable yield is nearly the same regardless of the effort ratio.

In the case where mixing is intermediate between the two extremes, $T_1 = T_2 = 0.56$ (Fig. 2, upper right panel) and $T_1 = T_2 = 5.6$ (Fig. 2, lower left panel) some very interesting relationships are implied from which several important scenarios can be derived. Depending on the effort ratio: (1) yield curves can be very flat-topped or descend rapidly with overfishing, (2) TMSY can vary widely at about the same level of total effort, and (3) the TMSY can be the same but at widely varying values of total effort.

Let us consider two scenarios where effort develops first on P_1 and then transfers in part to P_2.

Scenario 1

When the mixing rate is relatively low (Fig. 2, upper right panel) a fishery developing on P_1 would follow the dash-dot curve out to a maximum of 1.5 units of yield at 4–5 units of fishing effort. If 1 to 1.25 units of the 4–5 effort units were shifted to P_2, the equilibrium yield would increase markedly, and if an additional 1 to 1.25 units were transferred to P_2 the TMSY would be double that originally observed and for exactly the same amount of total effort. However, since the equilibrium catch rates differ between P_1 and P_2 at the same fishing effort (that of P_1 is one-half that of P_2) an unequal effort ratio would be trended towards.

When the mixing rate is moderately high (Fig. 2, lower left panel), the same manner of fishery development would have the opposite consequences. A fishery developing on P_1 would follow the dash-dot curve out to an TMSY of 3 units at 10 units of fishing effort. Any redistribution of fishing effort to P_2 would cause the total equilibrium yield to plummet.

Scenario 2

Development of a fishery on P_2 may occur through the addition of effort rather than through its re-distribution. When the mixing rate is relatively low (Fig. 2, upper right panel) development of a fishery on P_1 would follow the dash-dot curve. Additional effort being placed on P_2 could initially cause the overall fishery to begin following the dashed curve with increased equilibrium yield. Trouble would arise if total effort exceeds 8 units and greater effort were added to P_2 such that the effort ratio were even – total equilibrium yield would decrease. With a higher mixing rate (Fig. 2, lower left panel) the same trouble could occur, but it would occur at lesser effort being placed on P_2 than for the lower mixing rate situation.

SUMMARY

The formulation of the mixing model has considerable impact on the yield relationship. The model formulation presented here, along with the assumed parameter values, indicates that knowledge of the mixing relationship can be critical to good management, which can be highly influenced by the distribution of fishing effort (hence quota levels) among stocks. It remains to be seen, however, how well such a model can describe an actual fishery situation.

LITERATURE CITED

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Lord, G. 1971. Optimum steady state exploitation of a multispecies population with predator-prey interactions. *Cent. Quant. Sci. For., Fish. Wildl., Univ. Washington; Quant. Sci. Pap.* No. 29, 8 p. (mimeo.).

Pielou, E. C. 1969. An introduction to mathematical ecology. Wiley-Interscience, New York, 286 p.

7717

Response to the editorial on porpoise management, Vol. 2, No. 2.

Your recent editorial, "In Support of Rational Porpoise Management" (*Fisheries*, Vol. 2, No. 2), does much to further the exposure of the tuna-porpoise issue before our professional fisheries society. I am hopeful that you will receive many letters on this subject in response to your editorial. As the scientist responsible for the National Marine Fisheries Service's (NMFS) tuna-porpoise research program, but not speaking for NMFS, I heartily support much greater discussion of this issue as well as of marine mammal management generally under the Marine Mammal Protection Act (MMPA) before professional resources management societies. However, in my opinion your editorial could promote some misunderstandings or misconceptions and I would like to offer several observations to your readers.

The MMPA is a remarkably novel piece of conservation legislation that embodies an ecosystem approach to management. However, despite the MMPA's primary objective to ". . . maintain the health and stability of the marine ecosystem . . . ," the MMPA clearly and, in my opinion, unfortunately views the ecosystem from a strong bias in favor of only one component of the ecosystem—marine mammals. This bias undoubtedly resulted from the strong public outcry over such events as the clear overexploitation of many whale stocks and the harvesting with clubs of fur seals and harp seal pups which was perceived publicly as inhumane. The tuna-porpoise problem was a grafting onto the main bill. Implementation of the multiple management objectives of the MMPA has been very difficult, as has the conducting of research and the rendering of management advice. Partly this is because the management objectives of the MMPA, despite the word "PROTECTION" being prominently displayed in its title, are vague, contradictory, and partially incomprehensible (through the lack of precise and concise or generally accepted definitions and the grafted nature of the tuna-porpoise provisions). A rather wide range of actions is supportable under various sections and provisions of the MMPA.

Your first contention that heavy, one-sided pressure from "protectionist organizations and many private individuals" has tended to steer the current course of porpoise management within the sea of alternatives is undoubtedly correct because of the lack of a significant number of other voices on the issue; the exception of course is the tuna industry, but it is perceived as the "culprit." Also, a number of well-meaning, but perhaps over-zealous mammal scientists have helped to guide the present course. There is an obvious need for greater participation by professional resource management societies in the public debate over the issues created by the MMPA. As an indictment, not one such society has ever sent a representative to make an appearance at the hearings conducted by NMFS which establish the management procedures each year, and very rarely have any appeared before the many Congressional hearings held since passage of the MMPA. Those components of human society should be providing the support for a steady hand on the tiller. More communication and open discussion is the key to more effective representations of rational management.

The MMPA avoids use of the word "yield" as if it were some kind of taboo. The MMPA embraces a complex and ill-defined concept of an optimum sustainable population, for which NMFS has had to adopt an interim definition that is presently sufficient for working purposes. If a waiver of the general moratorium it places on taking[1] marine mammals is obtained, the MMPA permits and in fact may encourage harvesting to achieve the optimum sustainable population; in this context, the harvest is an optimum yield. However, for taking marine mammals incidental to commercial fishing operations (specifically tuna purse seine fishing in this issue) as opposed to a directed and purposeful harvesting, the MMPA has a totally different goal, that of reducing the incidental mortality and serious injury rate ". . . to insignificant levels approaching zero." This is a superbly humane and admirable goal from the viewpoint of preserving as much as possible an animal which is endeared to many people. On the other hand, it could be argued that the primary objective of the MMPA, ". . . to maintain the health and stability of the marine ecosystem," is being compromised by protecting as much as possible only one component (porpoises) of a complex ecosystem while harvesting large quantities of another very closely interrelated component, yellowfin tuna. Furthermore, there is the question of what is "insignificant"? (One animal per year? Low enough so that all significantly affected populations are growing? Low enough so that the optimum sustainable populations are maintained? Low enough so that certain people stop complaining?) Clearly more professional input to the public, Congress, and the management organizations would be extremely helpful.

As you pointed out, our progress in reducing incidental porpoise mortality by U.S. fishermen has been very good. The correct figures, however, are an estimated 104,000 mortalities in 1976 as opposed to 310,000 in 1971 and higher in previous years. For 1977 the stock-by-stock quotas total 62,429 animals. The kill of purposes per ton of yellowfin tuna caught this year stands at 0.26 as opposed to 0.9 for the same period in 1976 and 3.8 in 1971.

NMFS has declared the eastern spinner dolphins to be legally depleted under the MMPA, but at 55% of their initial size they show no signs of the "serious" depletion you mentioned. According to our current assessment the stock is healthy and is growing at a good rate. To further correct several statements in your editorial, the status of coastal spotted dolphins and Costa Rican spinner dolphins is unknown—taking in currently prohibited for both stocks. However, your statement on the status of offshore spotted dolphins, whitebelly spinners and the other 10 species or stocks of marine mammals involved in the tuna fishery are correct. While these assessments are the "best available scientific evidence," as required by the MMPA, I fully agree with you that further extensive research is absolutely required to evaluate several rather critical assumptions and to greatly improve our precision before we can be certain that our assessments are correct.

Your suggestion for the tuna fleet to retain and land all porpoises killed incidentally for use as food makes sense from the perspective of world food needs. This suggestion would also apparently satisfy many people who claim their only opposition to the porpoise mortality is that no apparent use is made of the dead animals; unfortunately they apparently do not care much about all the other creatures and plants of the sea which use and are "benefiting" by the mortality. However, the 5,000 to 7,000 tons round weight realized from 100,000 animals and considerably less in terms of edible weight would hardly be noticed in the world shortage of protein. From the perspective of health and stability of the ecosystem, could it be better to retain the material assimilated by porpoise in the eastern tropical Pacific ecosystem rather than to haul the insignificant amount away to North America or Asia? Additionally, U.S. policy is established by the MMPA and it prohibits, except for scientific purposes, the landing of incidentally caught porpoises without obtaining a waiver of the general moratorium.

Unfortunately, your statement, that landing the dead porpoises would not be an incentive to kill more and that the converse is true, is probably not correct. The U.S. tuna purse-seine fleet currently consists of about 121,000 tons of fish-hold capacity which makes about four trips per year for a potential annual capacity of nearly 500,000 tons. This fleet landed only about 300,000 tons of tuna and tuna-like fishes in 1976 (actually a record high) so a considerable tonnage in excess of the sustainable kill of porpoises could be brought in as an incidental catch without even denting the excess effective capacity of the fleet, much less denting the amount of capacity used to land the "high-value" tuna (yellowfin now brings 41¢ a pound landed value). The real benefit of landing all the incidentally killed animals is to research. We would have very precise estimates of the kill by species and stock, age and sex compositions, and health and reproductive conditions. This would greatly aid in rational management and take a lot of wind out of sails of others who want the fishery completely stopped using the excuse that "we do not know enough."

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[1] "Taking" under the MMPA is defined as harassing, hunting, capturing or killing or attempting to do so

Our current point estimate of the aggregated population levels of marine mammals involved in the eastern Pacific tuna fishery is 8.1 million, with an interval estimate of 4.4 to 12.1 million. With a few exceptions, these species are also found throughout the tropical and temperate latitudes of the world's oceans. Your calculations of the food consumption of marine mammals worldwide did not include the large whales, but serve to point out the need for considering—especially in the case of direct competitors for fishery resources—the marine mammals, an ecosystem approach to management of living marine resources. This concept is boldly emblazoned in the policy section of the MMPA, but is sadly misconstrued and misdirected in other sections of the MMPA, by protectionist organizations, by over-zealous mammal scientists, occasionally by our courts, and elsewhere.

The U.S. has achieved a remarkable record in reducing excessive harvesting of large whales and porpoises and in obtaining protection for certain heavily over-exploited marine mammal stocks. While there is still much to accomplish in this area, I believe that fisheries, wildlife and forestry scientists, long involved in rational management of living resources, should become involved professionally in the marine mammal issue to a significantly greater degree than they have in the recent past. The ecosystem tenet of the MMPA and the management objectives of the Fisheries Conservation and Management Act of 1976 need to mesh cleanly to provide for rational management of all living marine resources.

William W. Fox, Jr.
La Jolla, CA

7718

PHOTOGRAPHIC METHOD FOR MEASURING SPACING AND DENSITY WITHIN PELAGIC FISH SCHOOLS AT SEA

Few measurements exist of the spacing and density of fish within schools in the sea (Radakov 1973) although these characters have been well-studied in the laboratory (Breder 1954; Keenleyside 1955; Dambach 1963; Williams 1964; John 1964; Cullen et al. 1965; Hunter 1966; van Olst and Hunter 1970; Symons 1971). The density and spacing of fish within schools under natural conditions must be known if realistic fish abundance estimates are to be made from sonar survey data (Hewitt et al. 1976). This note describes a camera system that photographed fish schools at sea and a method used for estimating the density and interfish spacing from the photographs.

The camera system[1] consisted of an anodized aluminum casing which housed a spring-driven advance 35-mm camera, strobe light, and electrical components. The system was made watertight by creating a vacuum which sealed the acrylic lenses to the casing. Attached to the casing were a depth release with expendable chain ballast, floats, and a signal flag (Figure 1).

Upon immersion, the camera assumed an upright position, closing a mercury switch and starting an electric timer which activated the camera shutter and strobe light simultaneously. The system took 14 photographs per drop at set intervals of 24 or 48 s while sinking at a rate of 10

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[1] Designed by Daniel M. Brown, Scripps Institution of Oceanography (SIO) from an idea of John D. Isaacs, SIO. Blueprints are available at the Marine Sciences Development Shop, SIO.

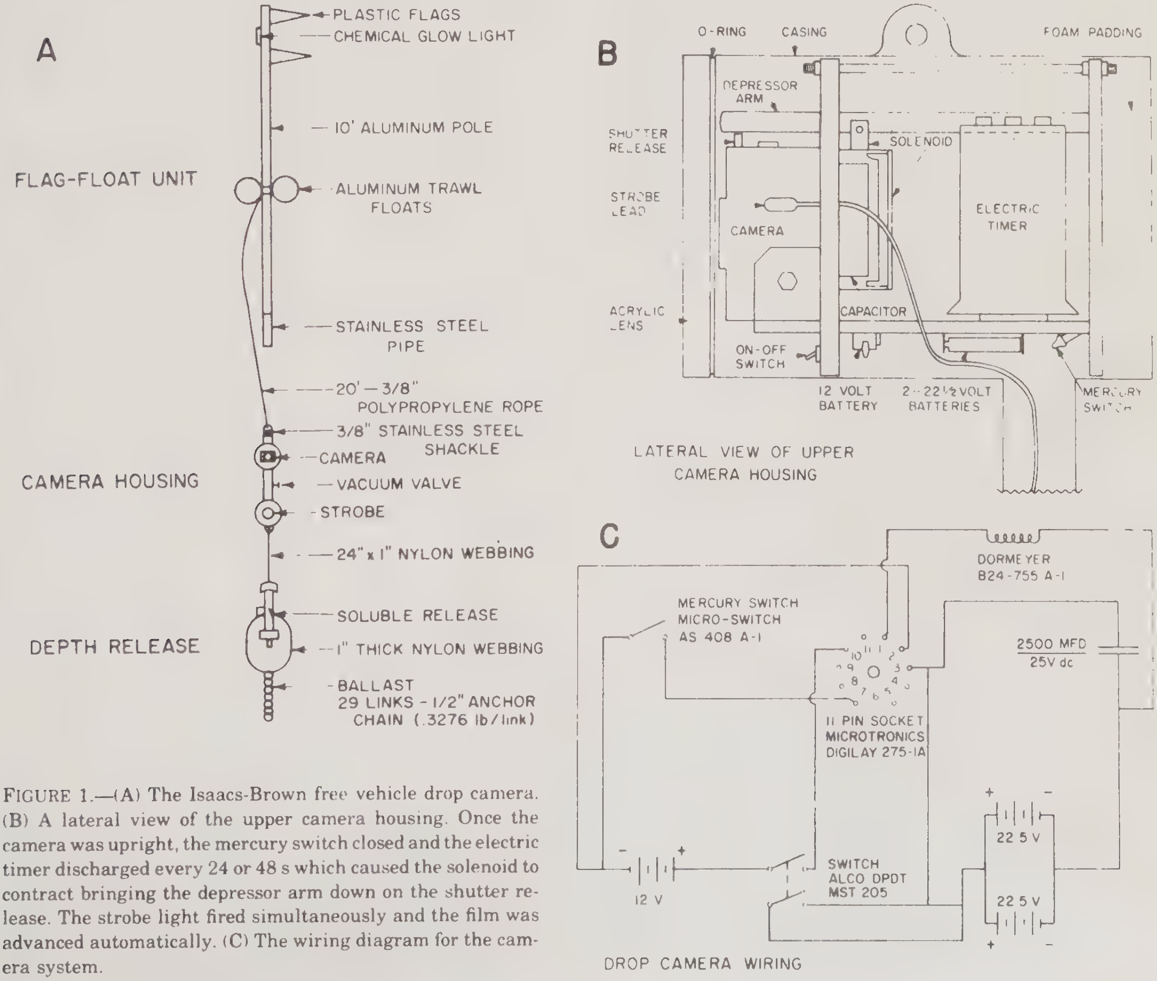
A
PLASTIC FLAGS
CHEMICAL GLOW LIGHT
10' ALUMINUM POLE
FLAG-FLOAT UNIT
ALUMINUM TRAWL FLOATS
STAINLESS STEEL PIPE
20' — 3/8" POLYPROPYLENE ROPE
3/8" STAINLESS STEEL SHACKLE
CAMERA
CAMERA HOUSING
VACUUM VALVE
STROBE
24" x 1" NYLON WEBBING
SOLUBLE RELEASE
DEPTH RELEASE
1" THICK NYLON WEBBING
BALLAST 29 LINKS - 1/2" ANCHOR CHAIN (.3276 lb/link)
B
O-RING
CASING
FOAM PADDING
DEPRESSOR ARM
SHUTTER RELEASE
SOLENOID
STROBE LEAD
CAMERA
ELECTRIC TIMER
ACRYLIC LENS
CAPACITOR
ON-OFF SWITCH
12 VOLT BATTERY
2 - 22 1/2 VOLT BATTERIES
MERCURY SWITCH
LATERAL VIEW OF UPPER CAMERA HOUSING
C
DORMEYER 824-755 A-1
MERCURY SWITCH MICRO-SWITCH AS 408 A-1
2500 MFD 25V dc
11 PIN SOCKET MICROTRONICS DIGILAY 275-1A
12 V
SWITCH ALCO DPDT MST 205
22.5 V
22.5 V
DROP CAMERA WIRING

FIGURE 1.—(A) The Isaacs-Brown free vehicle drop camera. (B) A lateral view of the upper camera housing. Once the camera was upright, the mercury switch closed and the electric timer discharged every 24 or 48 s which caused the solenoid to contract bringing the depressor arm down on the shutter release. The strobe light fired simultaneously and the film was advanced automatically. (C) The wiring diagram for the camera system.

m/min. At a preset depth, the ballast was released and the system returned to the surface.

Fish lengths were measured from photographic enlargements with an x-y coordinate reader and only those fish enclosed by a circle of 6 to 10 cm in diameter, drawn centered on the photograph, were counted in order to reduce computer processing time and peripheral photographic distortion. Repeated measurements of a photograph indicated a mean error in individual body length of 3.4% and a maximum error of less than 9.0% for any individual.

To estimate the distances from the camera to the fish it was assumed that all the fish were of the same size, were all oriented perpendicularly to the camera lens, and thus the differences in fish image size were dependent only on the distance from the camera. The distance between any fish and the camera was determined by calculating the ratio of the standard fish size to the 35-mm negative image size and substituting this value into the underwater calibration equation of the camera (Figure 2). The mean standard length of 12.0 cm (s = 1.9 cm) for anchovy in southern California waters (Mais 1974) was used as the standard fish size.

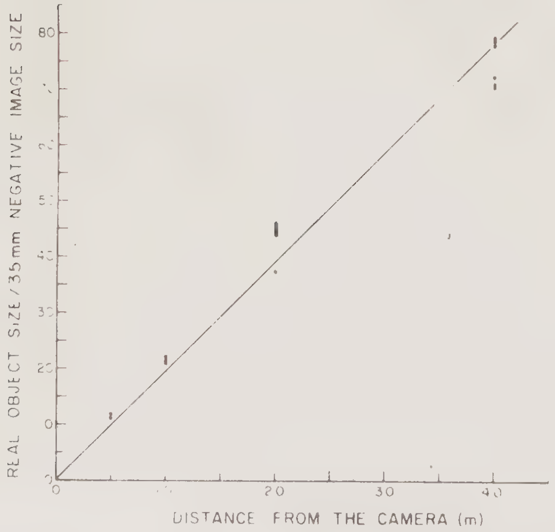

FIGURE 2.–The calibration curve for the Isaacs-Brown free vehicle drop camera. This camera system was calibrated under water by photographing objects of known sizes at fixed distances and the ratio of the real object to negative image size (y) was plotted against distance from the camera (x). The equation for the line is $y = 19.56x$. The distance to a fish was then determined by calculating the ratio of the standard fish size (12 cm) to the 35-mm negative image size of that fish.

A computer program calculated the lengths of the fish and produced a cumulative percent distribution of their sizes. One would expect the number of fish with small image sizes to increase with distance from the camera lens, but analysis revealed that a distance existed in most photographs at which the numbers of smaller fish failed to increase presumably because the more distant fish were not resolved owing to overlap, water clarity, and loss of lighting. An arbitrary limit was established at that image size by noting a change in slope on the graph of the cumulative percent distribution of fish lengths (Figure 3) and all fish smaller than the limit were not considered.

After establishing the minimum fish image size to be included in the program, a three-dimensional model of the photograph was constructed by calculating a third coordinate, z, based on fish image size and by adjusting the x and y coordinates for distance from the camera. The midpoint of each fish was then determined and a mean distance to the nearest neighbor was calculated by comparison with the midpoints of all the fish. The density of the school was computed by dividing the num-

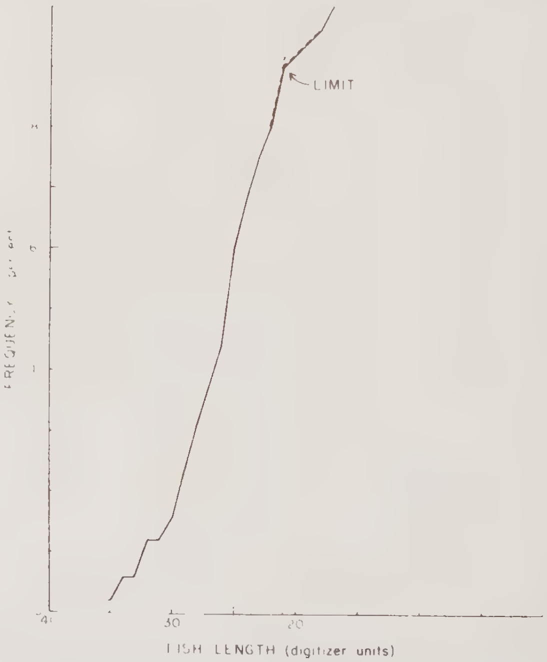

FIGURE 3.—The cumulative percent of length frequencies (in arbitrary units) for the fish measured in photograph 10 (Figure 4). Graphs of this form were made for each photograph analyzed in order to determine the distance beyond which all fish images were not resolved. The limit was made arbitrarily at the first apparent decrease in slope of the distribution.

ber of fish by the volume of the truncated cone between the planes of the largest and smallest fish image.

In September 1974, 14 camera drops were made in the Santa Barbara Channel on anchovy schools located by sonar. Observation of camera drops revealed that the slow sinking rate and $^1/_{1,000}$-s strobe flash did not disturb the fish. A space of about 4 m in diameter opened up in the school below the system as the camera descended. The increase in the school density caused by formation of the open space in the school was not detected in my analysis.

Anchovy schools appeared on 16 of the 230 photographs taken. For the 10 photographs in which the fish seemed to be perpendicular to the camera, the mean density of the school was 114.8 fish/m^3 where s = 99.1 fish/m^3 and the mean of the mean distance to the nearest neighbor was 1.2 body lengths with s = 0.3 body length (Figure 4, Table 1).

Photographs 6-10 were of the same school taken over a 10-min period. Excluding photograph 7, in which the fish appeared to be reacting to the camera or a predator and are more compact, the densities calculated for this school were 60, 56, 51, and 55 fish/m^3 with a mean distance to the nearest neighbor of 1.27, 1.28, 1.63, and 1.42 body lengths, respectively.

The interfish distances estimated for the schools photographed in this field study are, in general, larger than those reported in laboratory studies. This suggests that the small tanks used in these studies have caused fish to form more compact schools than they typically do under natural conditions.

The camera and these techniques could be of considerable value in determining the density and species composition of pelagic fish schools for sonar surveys. They should also be of value in the study of the behavior of schooling fish. School densities are known to change during feeding, predatory attack, and under diminished light intensity (Shaw 1970; Radakov 1973). Using the drop camera, it may now be possible to study the behavior of schools in the sea since interfish distance is as yet the best characteristic to measure changes in schooling tendencies.

TABLE 1.—Parameters of schooling compaction generated by the computer program for the 10 photographs in Figure 4.

Photo number	Fish/m^3	Mean distance (body lengths) to the nearest neighbor
1	100	1.24
2	174	0.84
3	78	1.38
4	50	1.35
5	366	0.79
6	60	1.27
7	158	0.86
8	56	1.28
9	51	1.63
10	55	1.42
Mean	115	1.20
Standard deviation	99	0.28

Acknowledgments

I thank Daniel M. Brown of the Scripps Institution of Oceanography for instructing me in the use of the camera; the California Department of Fish and Game for providing time on the vessel *Alaska* and the assistance of its crew; John Ford for assisting with the camera calibration; John Hunter, Paul Smith, and Roger Hewitt of the National Marine Fisheries Service for helping in various ways; and Evelyn Shaw and Charles Breder for reviewing the manuscript.

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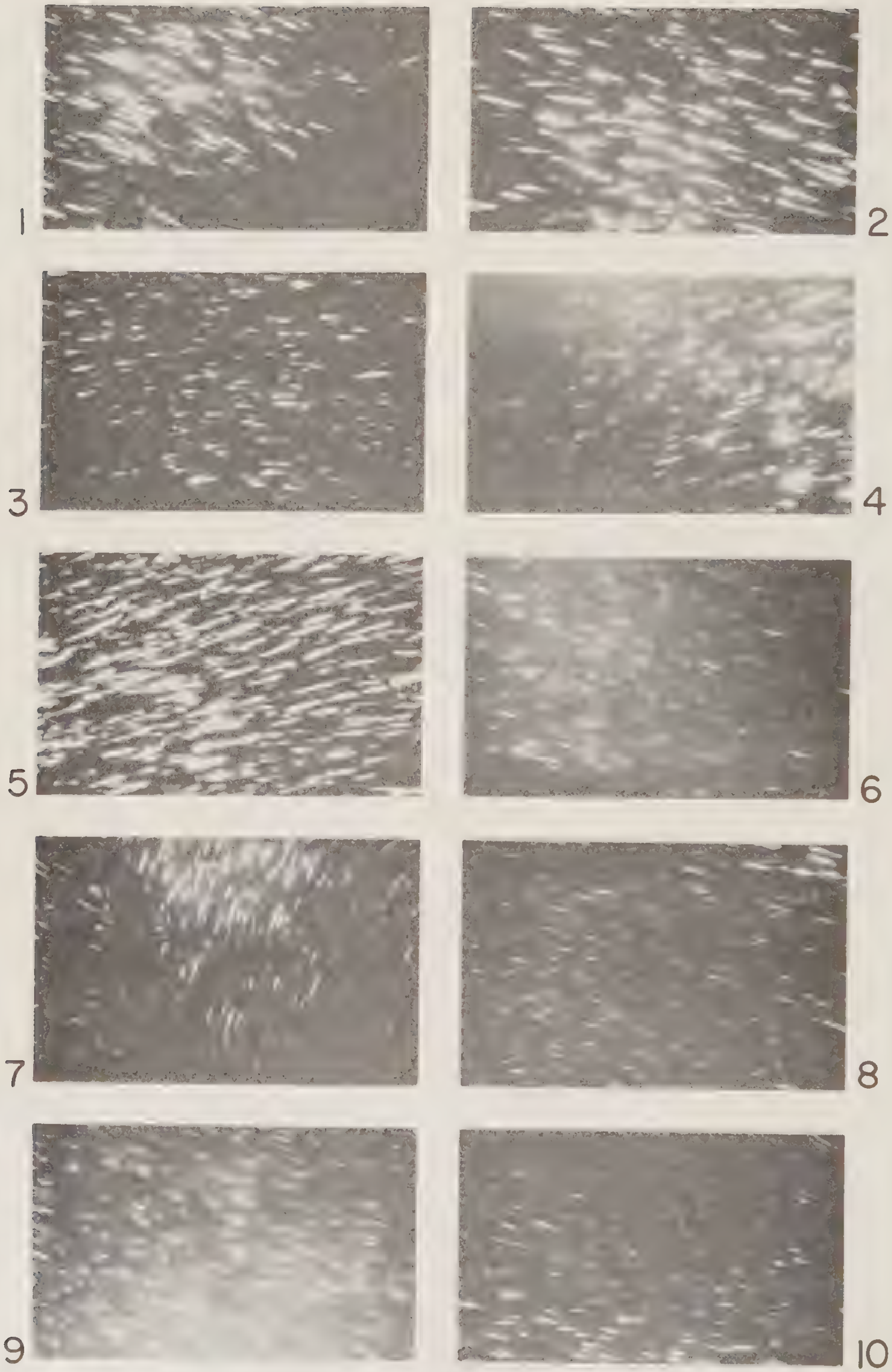

FIGURE 4.—Anchovy schools photographed in the Santa Barbara Channel with the Isaacs-Brown free vehicle drop camera during September 1974. Estimated fish density (fish/m^3) in each photograph, left to right, top row 100, 174, second row 78, 50, third row 366, 60, fourth row 158, 56, fifth row 51, 55.

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Biology of the Baitfishes *Herklotsichthys punctatus* and *Pranesus pinguis* in Majuro, Marshall Islands

THOMAS S. HIDA and JAMES H. UCHIYAMA[1]

ABSTRACT

The results of a baitfish scouting and sampling program carried out in the lagoon of Majuro Atoll, Marshall Islands, from May 1972 through April 1973 are presented in this report. The distribution and abundance, age and growth, maturity and fecundity, and stomach contents of the major baitfishes, *Herklotsichthys punctatus* (sardine) and *Pranesus pinguis* (silverside), are discussed. Adequate samples of baitfish could not be collected because of the apparent absence of suitable concentrations of the two major bait species, whose abundance fluctuated widely during the period of the observations.

INTRODUCTION

With the yellowfin tuna, *Thunnus albacares*, and skipjack tuna, *Katsuwonus pelamis*, probably being exploited at or near maximum levels in the eastern Pacific (Rothschild and Uchida 1968), there has been an increased interest in the skipjack tuna resources in the waters of the Trust Territory of the Pacific Islands where the Japanese operated a substantial fishery prior to World War II. During the prewar years, the Japanese vessels operated from bases in Palau, Truk, Yap, Saipan, Ponape, and Jaluit utilizing the available local baitfishes. There is very little information on the baitfish resources in the Trust Territory and since live-bait fishing for skipjack tuna is dependent upon the supply of baitfish, the National Marine Fisheries Service's RV *Townsend Cromwell* was dispatched to the area to assess this resource.

This project was undertaken as a result of findings made on three cruises of the *Townsend Cromwell* in 1971 and 1972. Of all island groups of the Trust Territory surveyed, the best baitfish concentrations observed during the cruises were in the Marshall Islands. A school of sardine, *Herklotsichthys punctatus*, seen in Jaluit Atoll on cruise 53 of the *Cromwell* (June-July 1971) was estimated to exceed 2.5 t and other schools of sardine and silverside, *Pranesus pinguis*, plus a few other bait species estimated at "several thousand" buckets (3.5 kg equals a bucket) were also seen (Hida 1971). Since the sardine and silverside were found to be in quantities suitable for conducting live-bait fishing for skipjack tuna, it was thought desirable to learn about the distribution, abundance, and biology of these species for management purposes.

Although the best concentrations of baitfishes were seen at Jaluit Atoll, Majuro Atoll was chosen as the site to carry out our baitfish observational program because it is serviced by a commercial airline and has the necessary facilities and supplies. Majuro Atoll, which is located in the southern part of the Marshall Islands, is roughly 32 km (20 mi) long and 6 km (4 mi) wide. Northeasterly and easterly trade winds prevail there and the weather is usually cloudy with the annual rainfall averaging about 356 cm (140 in). Surface water temperature and salinity samples taken at various places in the lagoon showed that temperatures ranged from 27.8°C in December to 32.8°C in June and that salinities were relatively stable ranging from 33.88 to 34.32°/₀₀.

OBSERVATIONAL PROGRAM

The sampling and observational methods used in this program were not ideal, but under the circumstances, the most feasible. Quarterly field trips were made by two or three observers from the Honolulu Laboratory for about 10 days per trip. The field trips were made in May, August-September, and November-December of 1972 and April of 1973. In addition, a resident Micronesian was employed to scout for and to sample baitfish on a weekly basis. In this way, the program was carried out continuously from May 1972 through April 1973. Observations were made each month except for July, when the Micronesian observer was ill, and October, because of adverse weather conditions.

SCOUTING METHODS

Scouting for baitfish was conducted in the lagoon close to the shoreline of Majuro (Fig. 1), usually from a 4-m skiff powered with a 20-hp outboard motor. Conditions for scouting were usually good during low tide except that maneuvering of the boat was difficult because of numerous exposed coral heads. The scouting runs, which covered most of the northeastern half of the lagoon as shown in Figure 1, were made daily during the quarterly visits. However, rough and murky waters or the necessity for carrying out other types of sampling did alter this routine. Occasionally, scouting was conducted from shore with an automobile. In this case, stops were made

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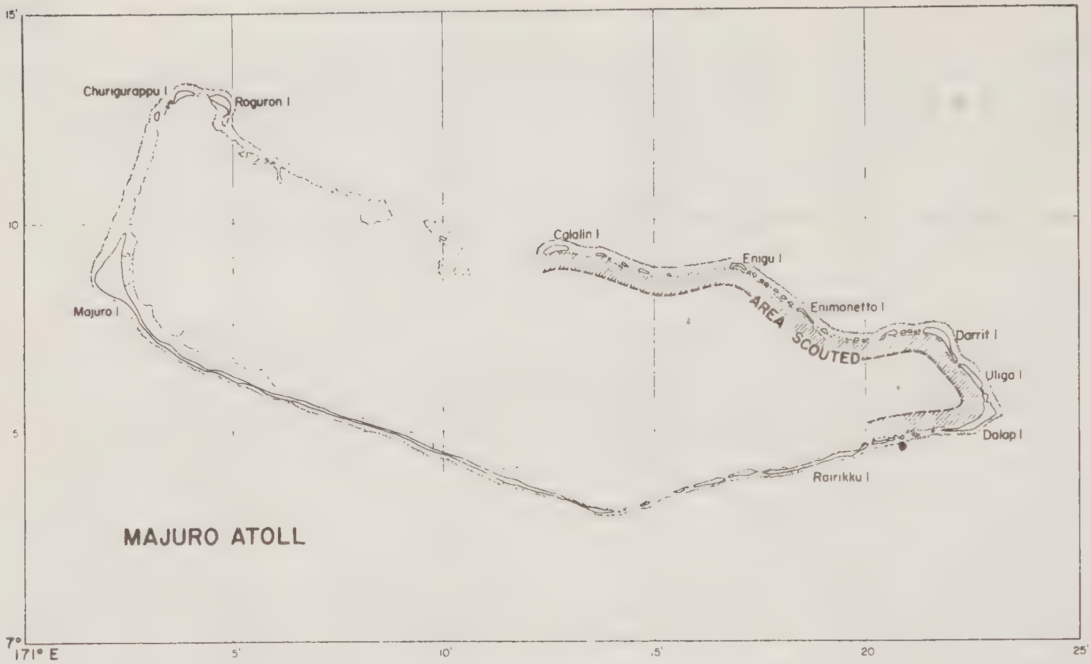

Figure 1.—Majuro Atoll, Marshall Islands.

frequently and whenever it was possible to gain access to a beach. About half a mile of shoreline was scouted on foot on these stops. The Micronesian observer did his scouting during weekends.

SAMPLING METHODS

Cast Net

Monofilament cast nets of 1.27 and 1.9 cm stretch mesh size were used to collect sardine and silverside during the scouting runs. Samples were collected whenever possible. The baitfish sampled were limited mostly to the larger sizes due to gear selectivity, especially in the case of the silverside. However, since there were usually only two observers, and because of the reefs and coral heads in the area, it was not possible to use a beach seine. The cast net was believed to be the most practical sampling gear under the circumstances. The collected samples were preserved in 10% Formalin[2] or 75% isopropynol and returned to the laboratory for examination.

Night-Light

During the quarterly visits, night-light stations were conducted by the field team with the skiff whenever the schedule allowed; a few were conducted by the Micronesian observer. Either a double mantle gas lantern or a 50-W bulb powered by a 12-V gasoline generator was used as the light source. Invertebrates and fishes that were attracted to the light were dip netted.

Handline

Small handlines were used to capture bigeye scad, *Selar crumenophthalmus*, which were usually attracted to the night-light together with other predators. The bigeye scad were sampled to see if they were feeding on baitfish. Their stomachs were collected and preserved in 10% Formalin for study at the laboratory.

Zooplankton Net

Fine meshed plankton nets, 20.3 and 45 cm in diameter, were towed by the skiff to sample zooplankton in the lagoon. Most of the samples were collected by the field team during the quarterly visits but a few were collected by the Micronesian observer. Tows were taken at the surface and at 5- or 10-m depths for durations of 15 to 20 min. Tows were made in the late afternoon, midmorning, or early evening hours. The occurrence of large numbers of large jellyfish at the surface at night precluded night tows. The samples were preserved in 10% Formalin and returned to the laboratory for study.

Trolling

Trolling was conducted during the quarterly visits by using a small spinner with a lure and a trolling rod and reel. Trolling was usually carried out routinely while heading out for the scouting grounds, but at times it was done directly into an actively feeding school of fish or around feeding bird flocks.

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

DISTRIBUTION AND ABUNDANCE

On cruise 53 of the *Townsend Cromwell*, June-July 1971, an estimated 2,500 buckets of silverside and 1,000 buckets of sardine were observed in Majuro lagoon. On *Cromwell* cruise 55, in November 1971, an estimated 800 buckets of sardine and 700 buckets of silverside were seen. In April 1972, on *Cromwell* cruise 57, it was estimated that there were about 1,000 buckets of sardine and silverside (mostly sardine) in Majuro. Most of the baitfish were seen in scattered schools in fairly shallow (2 m or less) waters along the eastern shoreline of the main island and along the many small islets on the northeastern part of the atoll. In May of 1972, on the first quarterly survey, about 100 buckets of sardine and 80 buckets of silverside were seen in scattered schools on the scouting runs. The largest school was estimated to consist of about 100 buckets of sardine and silverside. The baitfishes were often seen in quiet waters over fairly good seining grounds with sandy bottom and at times in areas with reefs and coral heads. Up until September 1972, a few small schools totaling about 50 buckets were seen on the scouting runs. The month of October was stormy and no observations could be made. From November 1972 through May 1973, there were no visible signs of baitfish concentrations in Majuro. Only a few small schools of fewer than five buckets of sardine and scattered small schools of silverside were seen. This study showed that the abundance of sardine and silverside in Majuro lagoon had apparently declined considerably since our first observations. Whether this apparent decline in abundance is an annual occurrence or whether this was an abnormal year is not now clear.

It is conceivable that the baitfish had moved out of the lagoon to other areas or into deeper or murkier waters of the lagoon where they could not be detected on our scouting runs.

Also, in May 1972, there was a Japanese fishing vessel conducting experimental live-bait, pole-and-line fishing in the Marshalls. They reportedly baited in the Marshalls, but where they caught the baitfish and how much they caught is not known. One of the ship's representatives said that an average of 200 buckets of sardine and, at times, as much as 500 buckets was taken in a single haul of a night net. If these amounts were taken out of Majuro lagoon with any frequency, it is possible that this would have affected the baitfish population during the period of our observation.

Our Micronesian observer also informed us that there was an unusual abundance of small kawakawa, *Euthynnus affinis*, in the lagoon in July of 1972. It was unfortunate that we were unable to find out on what these fish were feeding. Whether the occurrence of kawakawa in large numbers in the lagoon played a part in the "disappearance" of baitfish is again left to speculation.

As of November 1973, the Micronesian observer reported that the baitfish had not returned to Majuro. However, more recently, in April 1974, the baitfish apparently had returned to Majuro lagoon as well as to Jaluit Atoll (Robert M. Oka, former Honolulu Laboratory leading fisherman, pers. commun.).

AGE AND GROWTH ESTIMATES OF *HERKLOTSICHTHYS PUNCTATUS* AND *PRANESUS PINGUIS*

Because of inadequacies in sample size and in the size range (mostly 6.0 to 11.0 cm SL (standard length)) of baitfish specimens collected, growth estimates based on size-frequency mode progressions were not possible. Pannella (1971) provided indirect evidence of the presence of daily growth increments in fish otoliths. Struhsaker and Uchiyama (1976) have provided direct evidence that these increments are present in otoliths of the Hawaiian nehu, *Stolephorus purpureus*. Similar appearing structures are apparent in otoliths from *H. punctatus* and *P. pinguis* and for this study it was assumed that they are daily growth lamellae.

The largest *H. punctatus*, 10.92 cm SL, appeared to be 265 days old while *H. punctatus*, 8.62 and 8.69 cm SL, were estimated to be 189 days old. Specimens between 8.6 and 10.5 cm SL fell linearly (Fig. 2). The presence of the 10.92 cm SL specimen is an indication that growth decreases after 10.5 cm SL. The average growth in length was 0.35 mm/day for the specimens examined. *Pranesus pinguis*, 3.2 cm SL, was 112 days old. The largest specimen, 6.7 cm SL, was 265 days old. Other specimens fell linearly between these points (Fig. 2). The average growth in length was 0.227 mm/day. Interestingly, both species appeared to reach sexual maturity at the same age, between 6 and 7 mo.

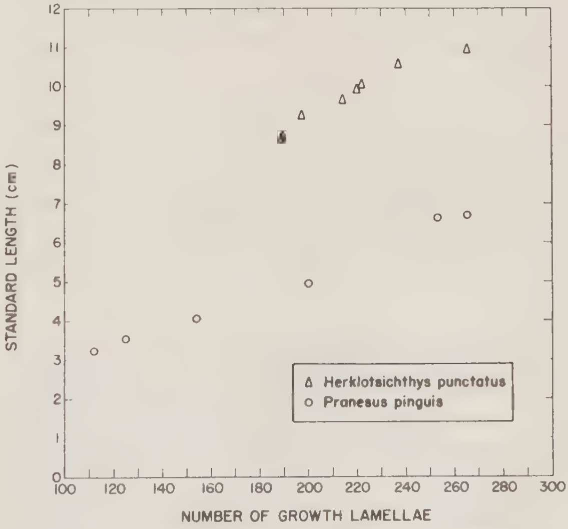

Figure 2.—The number of daily growth lamellae of ***Herklotsichthys punctatus*** and ***Pranesus pinguis*** otoliths plotted against standard length (cm).

MATURITY AND FECUNDITY

Material and Method

Specimens were pooled into groups by month of capture and then measured (SL) and the sex determined for sex ratio information. The ova diameters of the most advanced mode were measured and classified by appearance for maturity studies. Classification by appearance was believed to be more reliable than diameter measurements as shrinkage occurred during preservation in Formalin. The descriptions of the developmental stages of baitfish are the same as those used by Uchiyama and Shomura (1974) for swordfish (*Xiphias*) ova.

1. Primordial: ova diameters are less than 0.1 mm, transparent and ovoid.
2. Early developing: ova develop a chorion membrane, opaque yolk material deposits within the ovum, and ova are larger than primordial ova but less than 0.3 mm in diameter.
3. Developing: ova are completely opaque and spherical, chorion is stretched and not visible, and ova diameters range between 0.3 and 0.7 mm.
4. Advanced developing: ova have a fertilization membrane, a translucent margin around the yolk, and diameters range between 0.6 and 0.9 mm.
5. Early ripe: ova range between 0.7 and 1.0 mm in diameter, yolk material becomes translucent, and oil globules begin to form.
6. Ripe ova: ova are transparent, range in diameter from 0.9 to 1.1 mm, and oil globules are present.

For the fecundity study, the largest ovary of the month was examined. An attempt was made to keep the length of the fish constant. All ova in the most advanced mode were counted.

Sex Ratio

The sex ratios of sardine and silverside are presented as percentage of females in the monthly sample (Fig. 3). The percentage of female *H. punctatus* in the sample was highest in May-June and lowest in September. The percentage of female *P. pinguis* was highest in September and lowest in November.

Maturity

Since the number of specimens varied monthly, the percentage composition of the six ovarian developmental stages was used for comparison. *Herklotsichthys punctatus* appeared ready to spawn during April and May, as ripe ova were present in some ovaries. Ovaries at the developing stage occurred throughout the year but ripe ovaries were present only in April and May (Fig. 4). There were few *H. punctatus* under 7.3 cm SL in the samples and their ovaries were all immature. Ripe ovaries occurred in specimens over 9.0 cm SL.

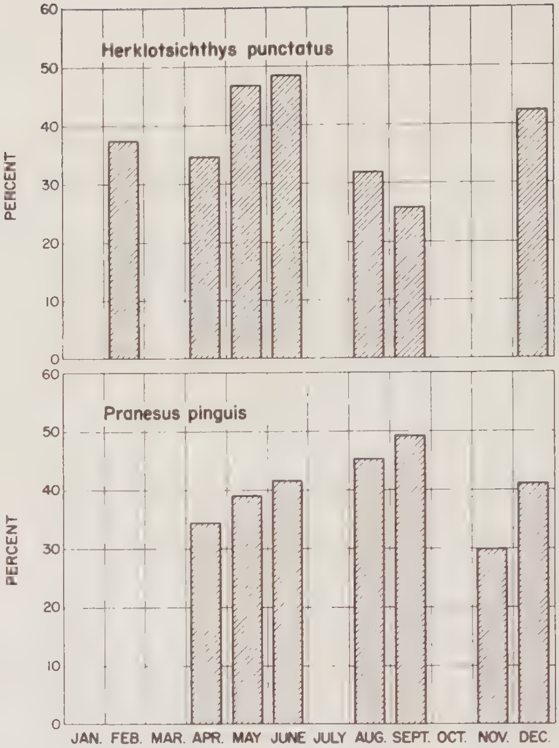

Figure 3.—Female component of monthly samples of Majuro baitfishes.

Ripe ovaries of *P. pinguis* occurred throughout the year. Spawning appeared to peak in August when over 80% of the ovaries contained ripe or early ripe ova (Fig. 3). The smallest silverside with a ripe ovary measured 5.5 cm SL.

Fecundity

Fecundity data are presented in Tables 1 and 2. The fecundity of *H. punctatus* ranged from 3,035 for a 9.3-cm specimen to 6,294 for a 9.8-cm specimen. There appeared to be a slight increase in fecundity from May through September. The fecundity of *P. pinguis* ranged from 272 for a 7.1-cm specimen to 852 for a 7.5-cm specimen.

STOMACH CONTENTS

Stomach contents of bigeye scad, sardine, and silverside were examined to see if they were feeding on juvenile baitfishes.

Bigeye scad were caught handlining from the skiff while carrying out night-light stations during August, September, November, and December 1972. Fifty-eight stomach samples were collected and examined. Among the principal food items were shrimps, isopods, ostracods, and fishes, especially of the family Bregmacerotidae (Table 3).

Table 1.—Fecundity of *Herklotsichthys punctatus* collected in Majuro.

Month (1972)	Standard length (cm)	Left ovary	Right ovary	Loose ova	Total	Maturity	Size range of ova (mm)
Feb.	10.2	2,610	1,381	151	4,142	Advanced developing	0.69-0.78
Apr.	9.3	1,840	1,171	24	3,035	Early ripe	0.86-0.94
May	9.8	3,294	1,790	33	5,117	Early ripe	0.90-0.98
June	9.8	4,508	1,663	23	6,194	Advanced developing	0.69-0.78
June	10.0	3,352	1,506	381	5,239	Early ripe	0.73-0.94
Sept.	10.6	2,322	2,821	10	5,153	Advanced developing	0.57-0.65
Dec.	10.6	3,243	1,161	0	4,404	Advanced developing	0.65-0.78

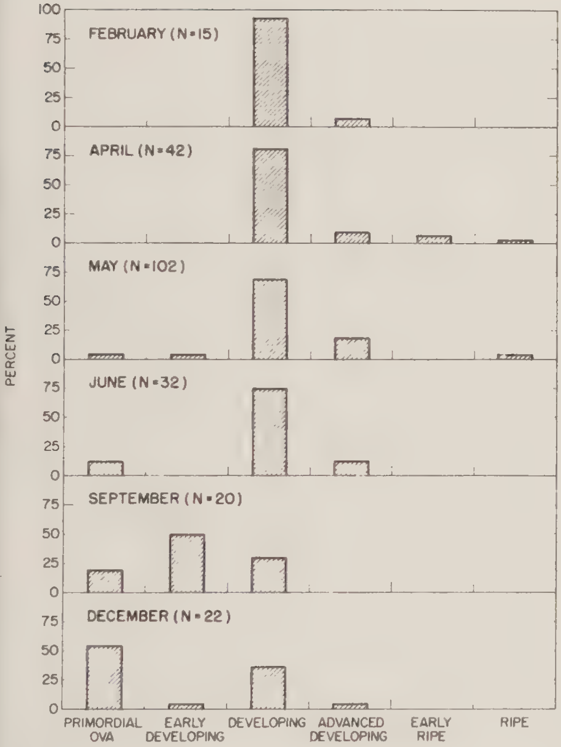

Figure 4.—Percentage of most advanced ovarian stages of *Herklotsichthys punctatus* by month (1972).

Table 2.—Fecundity of *Pranesus pinguis* collected in Majuro.

Month-year	Standard length (cm)	Fecundity	Size range of ripe ova (mm)
Apr. 1972	7.1	272	0.98-1.14
May 1973	7.3	504	0.98-1.14
Aug. 1972	7.4	504	0.82-0.94
Sept. 1972	7.1	624	0.78-0.98
Nov. 1972	7.5	852	0.82-1.10
Dec. 1972	7.0	558	0.82-1.14

Table 3.—Stomach contents of the bigeye scad, sardine, and silverside sampled in Majuro (x = present; xx = common).

Organisms	Bigeye scad	Sardine	Silverside
Polychaeta	x	—	—
Cephalocordata	x	—	—
Crustacea:			
Amphipoda	x	x	—
Decapoda:			
Crab megalopa	x	x	—
Shrimp	xx	xx	x
Lucifer	—	xx	—
Unidentified	x	—	—
Copepoda:			
Labidocera acutum	x	xx	—
Undinula vulgaris	—	xx	—
Unidentified	x	—	x
Euphausiacea	x	—	—
Mysidacea:			
Anchialina grossa	x	x	x
Siriella vulgaris	—	—	x
Unidentified	xx	—	—
Isopoda	xx	—	x
Ostracoda	xx	x	—
Mollusca:			
Gastropod larvae	x	x	—
Pelecypod larvae	—	x	—
Fishes:			
Acanthuridae	x	—	—
Atherinidae	x	—	
Balistidae	x	—	—
Bregmacerotidae	xx	—	—
Fistulariidae	x	—	—
Leptocephalus larvae	x	—	—
Syngnathidae	x	—	—
Unidentified	xx	—	x

About 50 sardine stomachs were examined. It was found that they fed on shrimps, lucifers, and copepods, especially, *Labidocera acutum* and *Undinula vulgaris* (Table 3).

About 100 silverside stomachs examined showed that their stomachs were essentially empty. This apparent habit of not feeding during the day was mentioned by Hobson and Chess (1973).

Examination of stomach contents showed that larval and juvenile sardine were not eaten by these predators at the time of our collections. It was hoped that larval and juvenile sardine could be obtained from stomach contents since our sampling methods were unable to capture them. Bigeye scad did feed on juvenile silverside but these could be sampled under the night-light. We were unable to catch enough silverside or sardine under the night-light to compare their feeding habits with fish caught during the day.

CONCLUSION

The inability to collect adequate samples during our field trips, largely due to the apparent absence of baitfish concentrations, left much to be desired in this study. However, we did find that the apparent abundance of *H. punctatus* and *P. pinguis* can fluctuate widely in Majuro. We also found that the two species reached maturity in about 6 to 7 mo at a size of 9 cm SL for *H. punctatus* and 5.5 cm SL for *P. pinguis*. From the presence of ripe ova in the ovaries, it seems that *H. punctatus* spawns in spring and *P. pinguis* throughout the year with a peak in August.

ACKNOWLEDGMENTS

We thank the observers that participated on the field trips to Majuro; Joe de Brum, our Micronesian observer; the staff of the District Administrator's Office for helping us with this study; and Denis C. K. Pang for doing the fecundity counts.

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Estimates of the Amount of Nehu, *Stolephorus purpureus*, Per Bucket of Bait in the Hawaiian Fishery for Skipjack Tuna, *Katsuwonus pelamis*

THOMAS S. HIDA and JERRY A. WETHERALL[1]

ABSTRACT

A sample survey in the Hawaiian pole-and-line fishery for skipjack tuna, *Katsuwonus pelamis*, showed that the average bucket of nehu, *Stolephorus purpureus*, the principal baitfish used in the fishery, weighs 6.4 kg (14.2 lb). This is greater than prior estimates for buckets of nehu (3.2 or 3.6 kg, 7 or 8 lb). It is not known whether the difference is due primarily to changes in bait handling practices or to inaccuracies in the early sampling and estimation procedures.

INTRODUCTION

Throughout the Pacific in the pole-and-line fisheries for skipjack tuna, *Katsuwonus pelamis*, the amount of bait taken aboard and subsequently used in fishing is customarily measured in units of "scoops" or "buckets." However, because bait handling practices differ among fisheries, and even among vessels in the same fishery, the average weight of bait per bucket or scoop varies widely. In the eastern Pacific a scoop of northern anchovy, *Engraulis mordax*, averages 3.6 kg (8 lb), while in Japan the average bucket of *E. japonica* varies from 3.4 kg (7.5 lb) to 7 kg (15.4 lb), depending on the area where observations are taken (Yoshida et al. 1977). Palauan skipjack tuna fishermen convey the local anchovy, *Stolephorus heterolobus*, in relatively small buckets with a high proportion of water, so an average bucket of bait in that fishery contains only 2 kg (4.4 lb) of fish (Muller 1977). In the Hawaiian pole-and-line fishery, the figure used historically for buckets of nehu, *S. purpureus*, is 3.2 or 3.6 kg (7 or 8 lb).

While many analyses within a particular fishery can be based on the amount of bait caught in terms of scoops or buckets, comparisons between fisheries require that the bait statistics be reduced to common units. Even within fisheries it is often necessary to know the actual weight of bait used. For example, this is critical in the evaluation of bait substitution schemes (Wetherall 1977).

We present results of a sampling program conducted in 1974-75 in the Hawaiian pole-and-line fishery with the objective of estimating the average weight of a bucket of nehu.

PROCEDURE

Observers sampled buckets of bait aboard cooperating skipjack tuna vessels during normal baiting operations. Buckets were sampled randomly. The baiting crews did not know which buckets were to be sampled until the baitfish were in the buckets and ready to be placed into the baitwells. Thus no bias was introduced by fishermen when loading the buckets. Two buckets were to be sampled from each of two sets on the designated baiting trips. Sampled baitfish were poured into a dip net and allowed to drain before being weighed with a spring scale to the nearest 0.1 kg (0.25 lb). Each sample was taken to the laboratory where the number of fish in a 0.5-kg (1-lb) sample was counted. Standard lengths of 50 specimens from each sampled bucket were measured. The stainless steel buckets on each vessel were measured and their volumes were calculated.

RESULTS

Although the response of vessel captains was good, scarcity of baitfish, rough seas, and drydocking of some vessels hampered the sampling, so only 13 samples were collected from five vessels. Results are given in Table 1.

The weight of nehu in the sampled buckets ranged from 3.2 to 10.4 kg (7.0 to 23.0 lb), averaging 6.4 kg (14.2 lb). The number of nehu per pound varied from 504 to 956 (averaging 725) and the estimated number of nehu per bucket ranged from 5,670 to 20,769 (averaging 10,414). The volume of the buckets used by the five vessels varied from 23.1 to 25.4 liters, averaging 23.5 liters (6.1 to 6.7 gal, averaging 6.2 gal).

Nehu are customarily bucketed directly from the bunt of the bait seine into baitwells, but since the mid-1960's a few vessels such as the *Anela*, the *Buccaneer*, and the *Lehua* have used a different procedure—nehu are dip

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Table 1.—The results of sampling buckets of nehu from five Hawaiian skipjack tuna fishing vessels.

Vessel	Date sampled	Bucket size (liters)	Set no.	Sample no.	Weight of nehu per bucket (kg)	Number of nehu per kilogram	Estimated number of nehu per bucket	Size range (standard length, centimeters)
Anela	2/21/74	23.1	1	1	5.21	1,235	6,434	3.1-5.3, mostly
			1	2	7.02	1,217	8,543	between 4.0 and 4.6
			2	1	5.10	1,147	5,850	
			2	2	5.10	1,111	5,666	
Kilohana	5/30/74	23.1	2	1	3.17	2,108	6,682	3.1-4.6, mostly
			2	2	4.76	2,000	9,520	between 3.3 and 4.0
			2	3	7.13	2,022	14,417	
Lehua	2/14/74	23.8	1	1	6.00	1,312	7,872	3.1-4.9, mostly
			1	2	7.36	1,435	10,562	between 3.9 and 4.3
Buccaneer	5/ 1/75	23.1	1	1	8.38	1,451	12,159	3.0-5.4, mostly
			1	2	6.57	1,865	12,253	between 3.0 and 4.7
Marlin	5/ 6/75	25.4	1	1	7.70	1,885	14,514	2.7-5.3, mostly
			1	2	10.42	1,991	20,746	between 3.2 and 4.6

netted from the bunt of the seine into buckets and then loaded into the baitwells. Our feeling is that the latter procedure results in less variability in the weight of nehu per bucket.

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MFR PAPER 1263

Report of a Colloquium on the Multispecies Fisheries Problem, June 1976

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INTRODUCTION

Historically, most fisheries have been managed as if populations of fishes are independent, even though many fisheries take more than one species together, often without distinguishing among them. There is concern that to manage effectively we must know how exploited populations interact with each other, with other elements of the environment, and with the fishery (and ultimately society) itself. This requires good data on each of the many species affected by the fishery, including those caught incidentally, and those seriously affected indirectly through biological relations with exploited species. Despite the general concern, however, efforts toward solution of what has been called the multispecies problem have been diffuse and uncoordinated. In fact, there is little evidence of a generally recognized broad concept, perhaps because so many variations of the problem exist.

To better define the multispecies problem, a colloquium was held at the Southwest Fisheries Center, Tiburon Laboratory, in June 1976. Under the sponsorship of the National Marine Fisheries Service, NOAA, this colloquium brought together investigators that represented a broad range of interests in fisheries biology and economics (Table 1). It was quickly recognized, however, that comprehensive solutions to multispecies problems transcend these fields to include political science, sociology, and the physical sciences. Thus, although the colloquium limited itself to topics that reflected the expertise of the attendees, it is emphasized that these topics are segments of a larger system that must be fully examined before final answers are attained.

The major components of the multispecies problem have long been recognized, but understanding their complexities has become possible only with recent advances in refined field techniques, computers, and quantitative fisheries research. Five interacting components can be identified within the system: management objectives, regulations, fleet or fishermen, exploited fish stocks, and ecosystems. The complexity of the interactions within this system, including areas within the expertise of the included research disciplines, is enormous (Fig. 1). This complexity is increased many fold by the continuously changing natures of the components. Therefore, even though the colloquium limited its attention to economics and fisheries biology, it faced a major challenge.

Table 1.—Participants in the Multispecies Colloquium.

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Peter B Adams	National Marine Fisheries Service, NOAA, Southwest Fisheries Center, Tiburon, Calif
Robin Allen	Inter-American Tropical Tuna Commission, La Jolla, Calif
William W Fox, Jr	National Marine Fisheries Service, NOAA, Southwest Fisheries Center, La Jolla, Calif
Edmund S Hobson	National Marine Fisheries Service, Southwest Fisheries Center, Tiburon, Calif
William H. Lenarz	National Marine Fisheries Service, NOAA, Southwest Fisheries Center, Tiburon, Calif
Loh Lee Low	National Marine Fisheries Service, NOAA, Northwest and Alaska Fisheries Center, Seattle, Wash
Roy Mendelssohn	School of Forestry & Environmental Studies, Yale University, New Haven, Conn
Virgil Norton	Department of Resource Economics, University of Rhode Island, Kingston, R I
Patric K. Tomlinson	Inter-American Tropical Tuna Commission, La Jolla, Calif.
Albert V Tyler	Department of Fisheries & Wildlife, Oregon State University, Newport, Oreg.
Carl J Walters	Institute of Animal Resource Ecology, University of British Columbia, Vancouver, B.C.
Norman Wilimovsky	Institute of Animal Resource Ecology, University of British Columbia, Vancouver, B.C.

The colloquium concentrated on identifying the types of research that could be expected to best benefit fisheries management, and immediately recognized that sound research programs would be unlikely without stable management objectives. Because management objectives determine the information needed, and thus research plans, changes in these objectives, amplified by the many interactions among the system's components (Fig. 1), could be profoundly disruptive.

IDENTIFYING RESEARCH AREAS

Before proceeding, the colloquium examined the relations among certain

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critical variables that characterize the diverse fisheries to be managed. A 3 × 3 matrix was constructed to do this (Fig. 2).

As illustrated by the matrix, the various fisheries can be assigned to one of the following categories: 1) a single-species fishery where only one species is taken in significant numbers, 2) a multiple-species fishery, where two or more species taken in significant number lack important interactions among them, and, 3) a multiple-species fishery where two or more species taken in significant number interact in important ways.

As further illustrated by the matrix, these fisheries can also be characterized by the types of gear used: 1) fisheries using specialized gear that takes a single species, 2) fisheries using flexible gear to take a species mix that can be altered during a given deployment, and 3) fisheries using inflexible gear to take a species mix thought to be unalterable.

It was recognized by members of the colloquium that these categories are artificial, and that the cells in the matrix are in reality points on continua. Also, it was recognized that few, if any, fisheries are characterized by any single point on the matrix. Furthermore, most fisheries can be expected to evolve under a wide range of varying pressures (economical, sociological, political, biological, and technological) that would change their positions on the matrix over time. Nevertheless, although the positions of most fisheries on the matrix are changeable rather than fixed, their characteristics at a given time center around specific points.

Further elaboration of the matrix (Fig. 3) shows the relationships among degree of management control, difficulty of determining sustainable yield, and the numbers of management options—all under the various combinations of biological and technological considerations defined above. Let us consider how the matrix might be used in planning research of management strategy. By examining the relationships shown, we can predict that a single-species fishery using specialized gear offers many management options

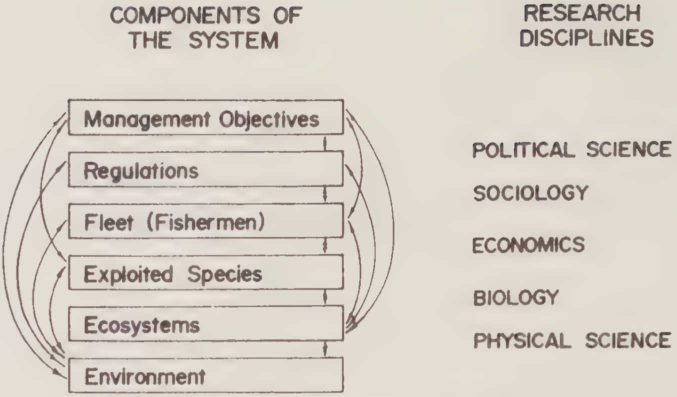
COMPONENTS OF THE SYSTEM
RESEARCH DISCIPLINES
Management Objectives
Regulations
Fleet (Fishermen)
Exploited Species
Ecosystems
Environment
POLITICAL SCIENCE
SOCIOLOGY
ECONOMICS
BIOLOGY
PHYSICAL SCIENCE

Figure 1.—Major components of the multispecies fishery problem.

FISHERY TARGET

▨	SINGLE SPECIES	MULTIPLE SPECIES	
		w/o interactions	w/ interactions
Specialized Gear			
Flexible Gear			
Inflexible Gear			

Figure 2.—Variables that characterize a fishery. Terms listed in the column at the left refer to the gear used.

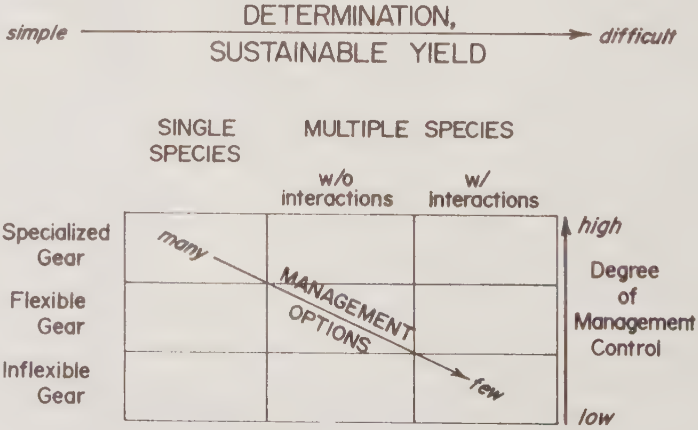
simple
DETERMINATION, SUSTAINABLE YIELD
difficult
SINGLE SPECIES
MULTIPLE SPECIES
w/o interactions
w/ interactions
Specialized Gear
Flexible Gear
Inflexible Gear
many
MANAGEMENT OPTIONS
few
high
Degree of Management Control
low

Figure 3.—Relationships among variables of a fishery.

and a high degree of management control. Under these circumstances it is relatively easy to determine sustainable yields and then implement management control if necessary—a highly desirable characteristic for management. Many fisheries, however, use what is in practice inflexible gear to take multiple species that interact significantly. Here, with few management options, and low degree of management control, the situation is unfavorable from management's point of view. Under these circumstances, management may wish to encourage more flexible fishing practices that permit greater selectivity in the catch, that is, introduce specialized methods that limit the catch to the target species. Unfortunately the fishing industry may resist these efforts through fear of increased cost or lost revenue. The histories of the International Commission for the Northwest Atlantic Fisheries and the International Pacific Halibut Commission include disputes over this issue. The fisheries involved exploit complexes of bottom and midwater fishes, and traditionally used methods and gear that took many incidental species. This resulted in dangerous stresses on species of relatively low abundance but of considerable importance to Canadian and U.S. fishermen. Some representatives of the fishery claimed the gear was inflexible, and the incidental catches unavoidable (perhaps to avoid management control). But Commission scientists, determining the gear was in fact flexible, introduced certain practices that relieved the pressures on the vulnerable species. They had, in effect, moved the position of the fishery on the matrix from row 3 to row 2 (Fig. 3), thus increasing the level of management control. Thus we see how examining the relationships illustrated by the matrix can provide insight and serve as a tool in planning research and management strategies where complex multispecies problems exist.

GENERAL NEEDS IN SOLVING MULTISPECIES PROBLEMS

Solving multispecies problems establishes research needs not unlike those that have shaped traditional single-species problems. The much greater complexities of the multispecies problems, however, require far more refined and sensitive methods and equipment. These needs can be arranged among five categories:

1) More effective data management systems.
2) More refined modeling techniques.
3) More accurate monitoring of existing fisheries.
4) More biological information on marine organisms (including species presently unexploited), with emphasis on biological interactions.
5) More emphasis on socioeconomic aspects of the problem.

Elaborating on each of these, in order:

1) Historically, data collected in some fisheries programs have been underutilized because more data have been collected than even a quantitatively trained biologist can handle. Increased use of computerized data management systems and consultation with data management specialists would allow more efficient storage and retrieval of the volume of data needed to solve multispecies problems.
2) Modeling has yet to fill its anticipated role as a major tool in solving management problems. To date, computer simulation models have generally suffered from poor structure and incomplete analysis, so that much of the behavior of the models remains unknown. In particular, optimization techniques should be more widely applied to better define those characteristics of the model that the modeler wishes to emphasize. What is needed, then, is further development and more systematic application of existing techniques, as well as the development of new techniques.
3) Monitoring fisheries. Characteristics of the catch (species, age, size) of most fisheries are poorly known, particularly where a large fishery is exploited by international fleets. Without this basic information we cannot effectively apply elementary procedures to assess even single-species stocks. Obviously, then, the more complex procedures needed to solve multispecies problems cannot be implemented with data presently available. More effective monitoring of the catch is a basic need.
4) To manage our marine resources effectively we must better understand the biology of marine organisms. It is especially important to understand the important interactions among the various organisms in the ecosystem, as only then can we hope to predict what the ultimate effects of a given management decision will be.

   In defining priorities for research there has been a tendency to ignore species currently unexploited by the commercial and sport fisheries. The following considerations point to some dangers in this course:

   a) The important, often critical, biological relations of most, if not all, species valued by fishermen are poorly understood or unknown, and at least many involve species currently unfished.
   b) Among the species currently unfished are opportunities for new fisheries that would reduce pressures now concentrated on the relatively few target species.
   c) Relative values change with time, and species without commercial value today may be highly valued in the future (including many forms now taken incidentally with a target species, but discarded because of low market value).
   d) To be effective, management programs must be designed with a long-range view. A

program locked into just a few currently favored species is soon likely to become obsolete.
 e) Responsibilities for managing marine resources extend beyond those species currently of direct importance to the commercial and sport fishing industries.

5) Socioeconomic problems may overshadow all other concerns of management and yet traditionally these areas have received relatively little attention. Although in many instances socioeconomic problems lie beyond the influence of management, they should be identified and anticipated in management tactics.

 Where the goals of management are merely preservation of a fishery, socioeconomic concerns have little impact; however, when management objectives expand beyond preservation, as often is the case, socioeconomic considerations generally are involved, and a relatively complex system of interacting influences must be evaluated. For example, when the concern is that of a specific fishery, economic considerations may impact on the system at several levels: 1) final demand (i.e., market prices), 2) production costs, and 3) harvesting effort. It is necessary to integrate biological information with the economic considerations at each of these levels, and a major problem is to identify the type of biological information needed in each case. The above is true of a single-species fishery as well as for a multispecies fishery, but for the latter the task becomes far more complex.

SUGGESTED RESEARCH

The kinds of research needed to solve multispecies problems can be arranged in three major categories according to the time required for their completion: 1) Short-term research projects are based on existing data (a) to provide approximations or "educated guesses" that respond to immediate needs, or (b) to provide guidelines for subsequent research; 2) moderate-term research projects usually involve collecting substantial amounts of new data and last 2 to 5 years, with a clearly defined termination date from the outset; and 3) long-term research programs usually involve collecting substantial amounts of new data that will influence the ultimate course of the research; such programs have an indefinite termination date, and generally last more than 5 years.

Recognizing these major categories, the group identified meaningful research topics that probe important multispecies problems. These topics are outlined below.

Short-Term Research

Synthesis of Existing Knowledge on Diversity and Stability of Disturbed Communities

In exploiting a species, or combinations of species, there is danger of reducing the diversity within certain marine communities. Although this may or may not be an undesirable situation, the impact of such a development remains unknown. Management should know if reduced diversity might lead to instability among valuable stocks, or if its options in future management decisions are being severely limited. Although answers will require moderate or long-term research programs, a preliminary step could be the synthesizing of existing knowledge on the relation between diversity and stability in disturbed communities.

Determination of Existing Fleet Capabilities

Management must be able to estimate the pressures that a fleet can exert in response to situations that could possibly follow management decisions. This is often difficult because many uncontrollable variables, most of them economic, influence the number of vessels active at any given time. The potential of the fleet must nevertheless be estimated because management efforts that increase catch per effort are likely to increase effort.

Immediate Stock Assessment

Extended jurisdiction responsibilities have created an urgent need for approximations of existing catch and effort records. These can only be based on existing catch and effort records, the literature, and conventional analytical techniques.

Identifying Whether a Multispecies Problem Exists

With simulation modeling, a short-term effort could compare the consequence of managing several exploited species as if they were one with the results of a more complex treatment of the individual species. This should provide insight into the need for extensive research on individual species and species interactions.

Preliminary Study of Program Design

Often the course, or even the feasibility, of a long-term effort cannot be determined without a preliminary study that considers program design and other factors. These studies can be considered independent projects, and should be more widely used to reduce the possibility of commitment to fruitless long-range research.

Moderate-Term Research

Surveys

Management requires understanding, and to understand an ecosystem one must know its biological and environmental components. Two types of surveys are needed: a) comprehensive surveys without bias toward species of current economic importance, and b) surveys assessing the status of species important to the fishing industry. The former type is more complex and would take a larger effort, but both could be completed in two to three years. The conclusions that can be drawn from each of these two types of surveys are different, and this distinction must be recognized by management.

Standardization of Fishing Effort

Fisheries that exploit more than one species with flexible gear present the need to partition effort among the species in order to estimate population abundance indices. Current methods of estimating population abundance require detailed records of catch and effort by time, area, species and mode of fishing. Data collection and/or data management systems must often be improved if this methodology is to be used.

Fleet Behavior Analysis

Behavior of fleets that use flexible gear to fish two or more species, shifting from one to another under differing circumstances, is difficult to predict, and this complicates management of the exploited species. Study of this behavior is needed. A monitoring program could compile the following data for each exploited species: catch per effort, value of catch, cost of effort, and catch limits. These data, considered with the cost of shifting from one species to another, could be analyzed with standard analytical procedures, such as linear programming. Intelligent interpretation of the results should permit predicting how the fleet is likely to react to management actions and other perturbations of the system.

Feasibility of Nonspecific Sampling

If preliminary study has indicated that it is unnecessary to consider individual species in a particular multispecies fishery (see previous section on Identifying Whether a Multispecies Problem Exists), an aggregation of species in the landings of that fishery might be sampled for age and size composition without identifying the component species. The results could then be compared with a statistical analysis of the same parameters from similar landings where the component species are separated and considered separately. From this comparison we may determine whether needed statistics can be compiled from landings where species are not separated. Possibly we can identify assemblages of species that respond as a unit to fishing pressures in a way that is consistent and repeated under measured applications of fishing effort.

Long-Term Research

Simulation Modeling

There is a need for imaginative and relatively simple models of biological communities. These must, however, incorporate a sound understanding of the biological interactions within these communities. This understanding has been lacking in the many attempts that have been made to model such communities, so it is not surprising that these attempts have failed. Although a model must be simple to have practical value in management, this does not mean the studies upon which it is based can be simple; to the contrary, simplicity in the model will come only with thorough study of the modeled situation.

Experimental Management Programs

Often it is difficult to evaluate the impact of management actions on the fishery owing to the inevitable effect of many uncontrolled variables. Consequently, it is desirable to conduct long-range experimental fishing programs that would test the effect of important management actions under controlled conditions. Among other requirements, such a program would need preserves where the experiments could be undertaken without interference from other fishing. Possible experiments include testing the impact on the populations of various modifications of fishing gear, size or catch limits, closed seasons, etc. In all such experiments, there should be sufficient time following actual manipulations of the system to monitor long-range effects.

Community Engineering

The construction of artificial reefs is one of the few areas where we have successfully influenced environmental change. Such reefs enhance sport fishing, and also permit study of disturbed communities. In addition to bettering the design of future artificial reefs, such studies will aid in predicting the impact of disturbances created by man, and also increase our understanding of natural reef communities.

Defining Communities

An important step toward meeting management goals is defining the communities of animals that include the exploited species. The concept of species assemblages (see section on Feasibility of Nonspecific Sampling) may be useful for management purposes as it may be possible to treat naturally occurring groups of animals as single species.

Stability of Ecosystems

One current theory suggests that stable ecosystems result from a particular combination of species in fixed proportions, and that such ecosystems become unstable if any one of its components is significantly disturbed. This theory should be further tested because, if true, fishing has far more impact on the ecosystem than has been assumed. Experiments with perturbed systems, such as artificial reefs and experimental management programs, could be designed with this test in mind.

Trophic Relationships

Many of the research programs suggested above indicate need to understand species interactions, and most, if not all, important interactions relate to feeding. Comprehensive understanding of trophic relationships within a community of animals is required to understand that community, and also provides valuable, often needed, background for other research.

CONCLUSION

To manage our fisheries effectively, we must develop long-range plans with stable objectives that recognize the need to understand the important interactions among resource species, other elements of the environment, the fishery, and, ultimately, society itself. To do this we need more effective data management systems and analytical techniques,more biological information, with emphasis on interspecific or intercommunity interactions, and more emphasis on socioeconomic aspects of the problem. Needed research ranges from short-term projects of fixed length, to long-term programs of indefinite length.

FUTURE MEETING

The colloquium closed with the participants unanimous in acknowledging the need for a future meeting. There was satisfaction in what had been accomplished, but recognition that it was just a beginning. Most important, it was recognized that the expressed views had been limited to those of fishery biologists and economists. The future meeting should include other viewpoints that are part of the multispecies problem, especially the views of physical scientists, political scientists, and sociologists.

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MFR Paper 1263. From Marine Fisheries Review, *Vol. 39, No. 9, September 1977. Copies of this paper, in limited numbers, are available from D822, User Services Branch, Environmental Science Information Center, NOAA, Rockville, MD 20852. Copies of* Marine Fisheries Review *are available from the Superintendent of Documents, U.S. Government Printing Office, Washington, DC 20402 for $1.10 each.*

BEHAVIOR AND SURVIVAL OF NORTHERN ANCHOVY *ENGRAULIS MORDAX* LARVAE

JOHN R. HUNTER

National Oceanic and Atmospheric Administration
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ABSTRACT

The object of this review was to provide an understanding of the behavioral factors that determine whether or not larvae of the northern anchovy, *Engraulis mordax* Girard, will starve. The swimming and feeding behavior of anchovy larvae is described and related to temperature, developmental stage, characteristics of the food and food distribution and to other variables. The principal sources of this information were published and unpublished observations of larvae cultured in the laboratory.

INTRODUCTION

Predation and starvation are considered by most specialists to be the dominant factors influencing survival of larval fishes. In the Southwest Fisheries Center (SWFC) of the National Marine Fisheries Service (NMFS), we have concentrated on the problem of starvation although some studies have been made on predation (Lillelund and Lasker, 1971; Theilacker and Lasker, 1974). The object of this review is to provide an understanding of the behavioral factors that determine whether or not an anchovy larva will starve. The swimming and feeding behavior of anchovy larvae is described and related to temperature, developmental stage, characteristics of the food and food distribution, and to other variables. The principal source of this information is observations of larvae cultured in the laboratory. Experimental design will not be given where information is already published, but a brief description will be given for new data. For information on laboratory culture of northern anchovy, the reader should consult Lasker, Feder, and Theilacker (1970), Theilacker and McMaster (1971), and Hunter (1976).

EGGS AND YOLK-SAC LARVAE

In southern California the major spawnings of anchovy occur in February and March but some spawning continues throughout the year (Lasker and Smith, 1977). During the height of the spawning season, temperatures in the upper 10 m vary from about 13° to 16° C.

Eggs are transparent oblate spheroids about 1.34 mm long and 0.66 mm wide, and are neutrally buoyant. Larvae hatch in 89.8 hrs at 13° C and at 59.8 hrs at 16° C (Zweifel and Lasker, 1976). The larvae at hatching averages 2.86 ± 0.028 mm standard length and weigh 0.0246 ± 0.0014 mg dry weight, of which 53% is yolk. At hatching larvae are nearly transparent, have no functional eye or jaw but olfactory and lateral line organs are developed (C. O'Connell, National Marine Fisheries Service, La Jolla, pers. comm.). After hatching, larvae are inactive; over 90% of the time they float motionless in the water usually with head directed downward. About once a minute they execute a burst of intense swimming, lasting about 1 to 2 sec. These bursts of activity may have a respiratory function as they occur regularly and increase in frequency when oxygen concentrations are below saturation (Hunter, 1972). The larvae have no functional gill filaments at this time so movement could serve to increase the transport of gases across the integument.

Owing to their inactivity, small size, and lack of a functional visual system, it appears anchovies in the yolk sac stage must be extremely vulnerable to predation. Indeed, Lillelund and Lasker (1971) showed that the copepod *Labidocera trispinosa* were 60% successful in capturing 1 day old yolk-sac larvae whereas success decreased to 11% for larvae that had begun to feed (4 days old). These authors also point out that success of capture seems to be correlated with the degree of activity of the larvae.

Development of a functional visual system and jaw, and nearly complete absorption of yolk coincides with the onset of feeding and a major increase in locomotor activity. Typically, larvae average about 4.0 mm standard length (SL) at this time but means vary from 3.8 to 4.4 mm depending on average egg size. The mean size of anchovy eggs varies seasonally, with larger eggs being more common in the winter (February and March) and small eggs occurring more frequently during the summer months (Lenarz and Hunter, MS). This seasonal variation would be expected to produce a seasonal trend in average larval size at first feeding. A larger size at first feeding would probably be of greater adaptive advantage in the winter months when cold temperatures produce slower growth rates than in the summer when it is more rapid.

SWIMMING BEHAVIOR OF POST YOLK-SAC LARVAE

Knowledge of swimming abilities of larval fish is essential for an understanding of survival. For example, the cruising speed of a larva will determine the frequency it will encounter prey, and determines in part whether or not a larva will remain in areas where prey are concentrated; also swimming accounts for most of the larva's energy expenditure. Burst speed capabilities determine in part the ability of a larva to avoid predation and plankton nets.

From the onset of feeding through adulthood, anchovy swimming consists of two types: continuously propagated caudally directed waves typical of most fishes that swim by caudal propulsion, and a series of bursts of motion consisting of a single tail beat followed by a rest or a glide. The beat and glide mode of swimming or intermittent swimming is used for cruising, whereas the other mode, continuous swimming, is used for high speed bursts. Nearly all swimming is intermittent in adult anchovy and in larvae after feeding begins. Continuous swimming in larvae is used for occasional bursts lasting usually less than a second and with a frequency of about 12 bursts/hour, less than 1% of the time devoted to swimming (Hunter, 1972).

Vlymen (1974) developed a model for energy expenditure of larval anchovy during intermittent swimming from theoretical considerations and analysis of cine photographs. He found that larvae of 14 mm standard length expended 5 x 10^{-3}cal/hr, and had a metabolic efficiency of 25%. This efficiency was high when compared to values obtained for larger fish and led Vlymen to speculate that this may have given anchovy larvae a competitive advantage over the Pacific sardine, *Sardinops caerulea.* It should be mentioned parenthetically, that although intermittent swimming may be more efficient, it is slow, and consequently the volume of water that can be searched for prey is less than that of a fish that swims in the continuous mode.

Swimming speeds of larval anchovy have been measured in various ways: plotting positions from cine photographs; counting tail beat frequencies; and visual approximation of larval position against a grid. For a temperature of 17° to 18° C the mean swimming speed of a 5 mm larval anchovy was 3.0 mm/sec using the photographic technique, 4.1 mm/sec using counts of tail beat frequency (Hunter, 1972); and 4.5 mm/sec when a grid was used (Hunter, unpublished data). These data set a range of cruising speeds of 0.6 to 0.9 body lengths/sec for anchovy larvae at 17° to 18°C. Maximum bursts of speed, on the other hand, appeared to be about 15 body lengths/sec but swimming in this case is continuous rather than intermittent and can be sustained for only brief periods (Hunter, 1972).

Although it is clear that larval size is a significant determinant of speed, the methods used to measure speeds of larvae, however, are not sufficiently accurate to establish the correct length coefficient. To do this larvae must be subject to known water speeds. Consequently, to adjust for size, the convention of dividing speed by length has been followed (Bainbridge, 1958), but it should be recognized that the true coefficient is probably less than unity (Brett, 1965). In addition to size, cruising speeds are influenced by many other variables, thus the above averages can be considered only to be general estimates.

Temperature, age, food distribution, feeding activity, and condition of the larva all influence swimming speed. Speed declines in starving larvae until they remain almost motionless, floating head down in the water. Food distribution may have several effects on swimming speed. In dense patches of food (*Gymnodinium splendens*) speed declines by about 60%. On the other hand, at any given density the larvae that are feeding at the highest rate are generally the ones that are swimming the fastest (Hunter and Thomas, 1974). This latter effect might be caused by the physical state of the larvae. For example, within a given food density the healthy and presumably better fed larvae are the most active and feed most often.

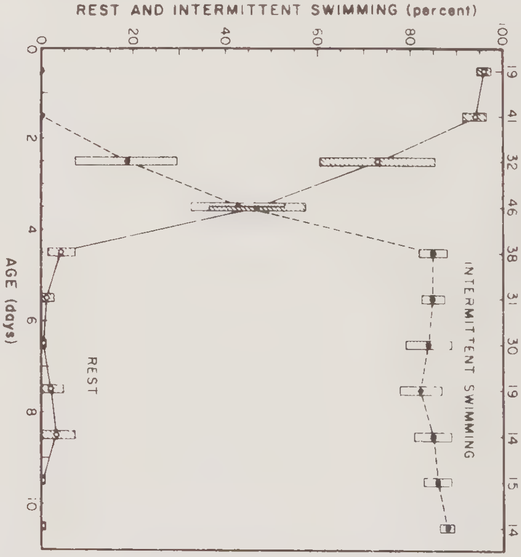

FIGURE 1. The proportion of time spent in rest and intermittent swimming by anchovy larvae during the first 10 days of larval life at 17° to 18° C (from Hunter, 1972). Points are the mean percent ± 2 X SE; the number of observations (N) is given at top of graph.

Temperature affects rate of development which, in turn, affects the age at which the transition occurs between occasional bursts of swimming typical of yolk-sac larvae to the almost continuous intermittent swimming typical of larval and adult anchovy. This transition is shown for the temperature range of 17° to 18° C, and indicates that by age 5 days the proportion of time spent in intermittent swimming becomes nearly constant (Figure 1). More recent data show how temperature determines the time at which this transition is made. The very low swimming speeds at 13° C (Figure 2) indicate that the transition did not begin at age 4 days, whereas the transition had started in larvae in 14° C water, and was almost complete in 4 day larvae in 17.5° C water. By age 6 days, larvae at all temperatures have completed the transition. The data indicate a direct temperature effect on swimming behavior as well. At ages 8 to 12 days larvae reared at temperatures less than 16° C appear to swim at a slower speed than those above 16°C.

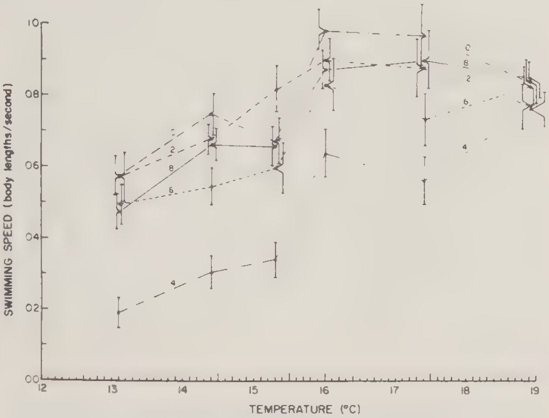

FIGURE 2. Swimming speed in body length/sec for anchovy larvae reared at five different temperatures. Speed was measured at ages 4, 6, 8, and 12 days by visual approximation of larvae against a grid; points are means ± 2 X SE (bars); numbers are age in days. All larvae were reared on *Gymnodinium splendens*.

In summary, size, temperature, food distribution, and starvation all influence cruising speeds. It is the complex interaction of these variables that determine whether or not a larva will find food and survive. Cooler temperatures cause a reduction in activity and therefore, in metabolic demand; on the other hand, cold temperatures result in slower growth and greater exposure to predation during the larval phase.

ENERGY SPARING MECHANISMS

Mechanisms that reduce activity and thereby conserve energy are probably important in the survival of larval fishes. Two possible mechanisms have been mentioned previously in this report: the reduction in activity associated with high food density; and the reduction in activity associated with colder water temperatures.

Another possible energy-sparing mechanism was proposed by Uotani (1973) for a Japanese anchovy and sardine, presumably *Engraulis japonica* and *Sardinops melanosticta*. Uotani found that net captured larvae of both species had expanded gas bladders at night and deflated ones in the day. He proposed that inflation at night was an energy sparing mechanism. He also suggested it might be effective in reduction of predation at night.

This behavior was examined for the northern anchovy, *Engraulis mordax*, in the laboratory by measuring the width of the gas bladder at night and during the day[1]. Larvae were maintained under a 12 hr light-12 hr dark cycle without a dawn or dusk transition in illumination. The width of the gas bladder of larvae collected in the dark and in the light was measured for nine, 0.5 mm length classes for larvae 8.5 to 15.4 mm SL and statistical comparisons were made between dark and light samples for each length class using the Mann-Whitney U test (Siegel, 1956). Larvae 8.5 to 9.4 mm showed no difference in gas bladder width in the dark from the light (P = 0.78) while larvae 9.5 to 10.4 mm differed at P = 0.035, and the remaining seven length classes differed at P 0.001. Thus, the threshold larval length for filling the bladder at night occurred between 9.5 and 10.4 mm corresponding to the intersections of the regression lines for bladder width on length for larvae in the dark and light (Figure 3). In this comparison, only data from larvae collected in the middle of the day were used because a transitional period of 2 to 4 hours occurs in the morning after the onset of the light (Figure 4). The change in light intensity would be expected to be much slower for larvae in the sea than in this laboratory experiment and thus deflation of the bladder is probably not a critical problem. In the dark, larvae with inflated bladders were suspended motionless, head downward, until disturbed by the light used to see them. The bladders were frequently so distended at night that they constricted the gut, a feature noted by Uotani (1973) in field caught larvae. The most tenable explanation of diel change in bladder size is that it permits the larva to adjust to neutral buoyancy at night and thus to conserve energy. It might also be useful if it enabled the larva to remain at about the same vertical position in the water column at night.

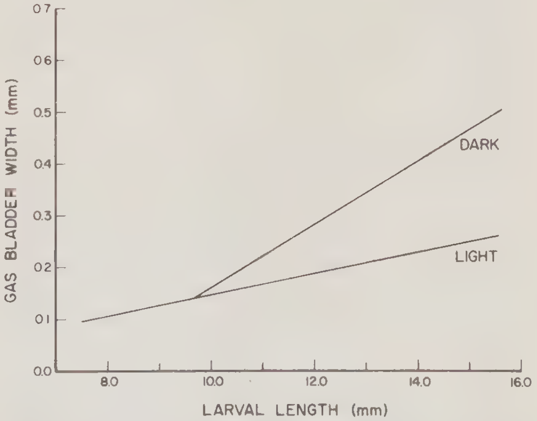

FIGURE 3. Regression of width of gas bladder in the dark (Y) on larval length (X) is Y = 0.613 X −0.453 and standard error of the estimate, s_{yx} = 0.0785; the regression of width of gas bladder in light on larval length is Y = 0.203 X −0.0556 and s_{yx} = 0.038.

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[1] This work has been described in detail by Hunter and Sanchez (1976) after this paper was submitted for publication.

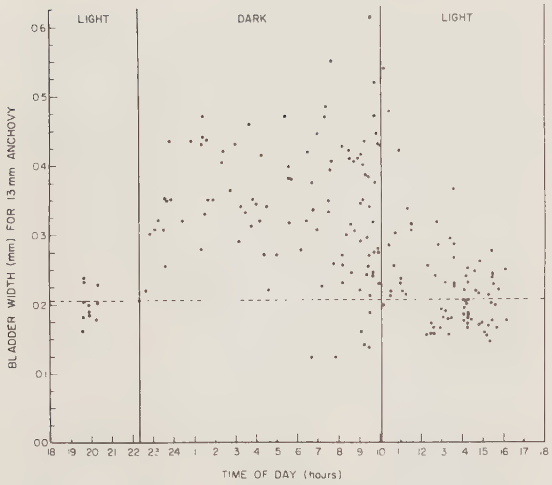

FIGURE 4. Diel change in width of gas bladder for anchovy larvae 13 mm SL. Larvae in sample ranged in length from 12.0 to 15.4 mm SL. Gas bladder width was adjusted to a common length, 13 mm, by using regression equations given in Figure 3.

FEEDING BEHAVIOR

Studies of the feeding behavior of larval anchovy provide insight into the conditions at sea that would favor starvation or growth. A complex of interacting variables determine if a larva will respond to a prey and whether or not it will find enough food to survive. Starvation, temperature, stage of development, time of day, larval size, prey size, feeding success, swimming speed, sighting range for prey, prey visibility, prey avoidance behavior, prey distribution and density may affect the amount of food ingested directly, and may affect it indirectly through interactions with other variables. Some information exists on the direct effects of some of these variables but little information exists on possible interactions.

Description of Feeding Behavior

On the average, larval anchovy first react to a prey when it is about 0.4 body length from the head of the larva. Upon sighting a prey the larva forms an S-shaped posture and advances toward the prey by sculling the pectoral fins and undulating the finfold, while maintaining the S-posture. When the prey is about 0.07 body length from its snout, the larva opens its mouth and straightens its body. This causes the body to drive forward, and the prey is ingested. The prey is maintained in the center of the binocular field while the fish is in the S-posture by slight adjustments in the position of the head and body. The entire act requires 1 to 2 seconds.

Time of Day and Satiation

Larval anchovy feed during the day and not at night, at least during the first half of larval life. Rods are not present in the retina in noticeable numbers (C. O'Connell, National Marine Fisheries Service, pers. comm.) until 20 days of age (11 mm SL). That larval anchovy feed only during the day is supported by my laboratory observations and also by field data described by Arthur (1956) who examined the stomach contents of sea-caught larvae 3 to 12 mm in length. In addition, stomach content analysis of adult anchovy also indicate that adults feed primarily during the day (Loukashkin, 1970).

In the laboratory, larval anchovy do not cease feeding once the gut is filled. Larvae with filled guts, sometimes with a fecal pellet protruding from the anus, can be seen feeding throughout the day. Thus satiation probably does not occur during the early portion of larval life, but it may occur after the larva reaches 18 to 20 mm and schooling begins. Satiation does occur in adult anchovy (Leong and O'Connell, 1969).

Starvation

Feeding declines with starvation until a point is reached where larvae are unable to feed sufficiently to maintain life although they may live a number of days after they reach this point. First feeding larvae reach this point 2.5 days after yolk absorption (Lasker, et al, 1970). At metamorphosis, on the other hand, anchovy are able to withstand starvation for over 2 weeks and survive when given food (Hunter, 1976). Thus, there exists a dramatic change in the ability to withstand starvation over the larval period ranging from 2.5 days for first feeding larvae to 2 weeks for newly metamorphosed anchovy (35 mm SL).

Temperature

The effect of temperature on feeding behavior in anchovy 4 to 12 days old was recently examined. For this survey I selected data on feeding behavior from rearing experiments conducted at a variety of temperatures in which the lengths of the larvae were about the same. Owing to different growth rates at different temperatures the ages of larvae are different but all were grown at high food densities in excess of 200 *Gymnodinium splendens* cells per ml. Only larvae greater than 4.5 mm or larger are considered because the stage of development influences feeding rate for smaller larvae and developmental stage is also a function of temperature. Feeding activity was measured by counting the number of feeding strikes executed by a larva in 5 minutes. Observations were made on 3 to 4 groups of larvae at each temperature and usually 15 observations per group per day. The data show that for larvae of similar length, and thus similar weight, feeding rates are higher for higher temperatures (Table 1). Thus the effect of temperature on feeding coincides with that on activity, indicating increased metabolic demand at higher temperatures. The feeding rates observed are, in general, quite high at all temperatures. This is because the larvae were feeding on a prey, *Gymnodinium splendens,* that is less than optimal in size, a point I shall return to in more detail later.

TABLE 1

Average Feeding Strikes per Minute and Mean Length of Anchovy Larvae Reared on *Gymnodinium splendens* at Various Temperatures.

Temp. °C	Age (days)	Length mm ± 2 × SE*	Feeding strikes/min ± 2 × SE*	Age (days)	Length mm ± 2 × SE*	Feeding strikes/min ± 2 × SE*
13.1	12	4.7 ± 0.1	3.1 ± 0.6	—	—	—
14.4	10	4.6 ± 0.1	4.3 ± 0.8	12	5.0 ± 0.1	4.7 ± 0.6
15.3	10	4.6 ± 0.1	3.3 ± 0.6	12	5.0 ± 0.1	4.1 ± 0.7
16.0	8	4.8 ± 0.1	4.1 ± 0.8	10	5.0 ± 0.1	4.3 ± 0.9
17.4	6	4.5 ± 0.1	4.8 ± 1.0	8	5.0 ± 0.1	5.9 ± 0.9
18.9	6	4.8 ± 0.1	7.0 ± 1.0	8	4.9 ± 0.2	7.7 ± 1.3

* SE = Standard error.

Density and Distribution of Food

Larval anchovy feed less often at lower food densities than at higher ones. Food density, however, also alters the structure of the search pattern for food. Larvae that enter a dense patch of *Gymnodinium* reduce speed, and alter the directional characteristics of their search pattern. In a dense patch they swim directly ahead less frequently and make more 180° turns than they do when the density is lower. The result of these changes in search pattern is a reduction in the area covered while searching for food if the food is highly concentrated and an increase in area covered when it is not. In other words, larvae respond kinetically to a food distribution which results in the larvae remaining in areas where food is more dense (Hunter and Thomas, 1974).

Feeding Success

At the time of first feeding, larvae are much less successful in capturing prey than they are later in life. This pattern has been observed in herring and other larval fishes (Rosenthal and Hempel, 1970). Larval anchovy capture about 10% of the food at which they strike at the time of first feeding but this value increases to about 90% when they are 20 days old (Hunter, 1972). This observation suggests that larvae are more vulnerable to starvation at the time of first feeding than later in development.

Characteristics of Prey

The characteristics of the prey such as size, nutritional value, digestibility, visibility, avoidance behavior, and the presence of protective devices such as spines must be important elements in the survival of larval fishes. The importance of most of these characteristics to marine fish larvae have not been evaluated. There is some evidence that digestibility may be important. For example, *Artemia salina* nauplii are ingested by herring and anchovy larvae but they fail to digest them completely and grow slowly or die when fed an exclusive diet of *Artemia* (Rosenthal, 1969; Hunter, 1976). Once a larval anchovy develops a differentiated gut, however, they are able to grow and survive on *Artemia* nauplii. In addition, evidence exists that first feeding anchovy larvae do not survive or grow slowly when fed some species of thecate algae whereas they are able to survive when fed unarmored dinoflagellates such as *Gymnodinium splendens* (Lasker et al., 1970). Thus, the straight tube gut, characteristic of young larval clupeoid fishes, may restrict these fishes to food that may be easily digested. Such potentially indigestible items as copepod eggs and diatoms which are found in guts of anchovy larvae (Arthur, 1956) may contribute little to growth or survival.

Prey size is the only other characteristic for which some evidence exists on the importance to larval survival. Culture techniques for all larval fishes require that prey size be increased as a larva grows. Most studies of foods ingested by larvae indicate that prey size increases with larval length. This has been shown for larval anchovy by Berner (1959) and Arthur (1956).

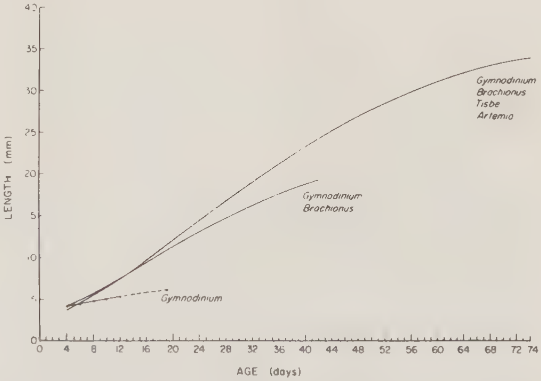

FIGURE 5. Growth of anchovy larvae fed different foods at 16° C. Foods used in rearing are given at end of each curve. Top, Laird-Gompertz growth curve for anchovy through metamorphosis and fed a graduated series of foods; middle, Laird-Gompertz growth curve for larvae fed only smaller foods (*Gymnodinium; Brachionus*); bottom, the curve connects mean lengths for ages 4 to 20 days for larvae fed only *Gymnodinium.* Densities for the same food are comparable in all experiments. Data and parameters for the first two curves are given by Hunter, (1976); data for the last curve are unpublished (n = 120 larval lengths per point; results are from eight rearing experiments; the last point, age 19 days, is from Lasker et al. (1970)).

The importance of increasing prey size with growth is illustrated by comparing growth rates of larval anchovy fed different foods (Figure 5). When larvae are fed *Gymnodinium* alone, growth becomes asymptotic at about 6 mm, whereas, when *Gymnodinium* and the rotifer *Brachionus plicatilis* are used, growth becomes asymptotic at about 20 mm and few larvae survive. A heavy mortality occurs in larvae fed only *Brachionus* and *Gymnodinium;* survival drops from 46% at age 26 days to 6% at age 42 days. On the other hand, if larvae are given, in addition to these foods, copepodites and adults of *Tisbe* sp., and *Artemia* nauplii when the gut becomes differentiated, larvae can be grown through metamorphosis with a reasonable survival, 12.5% at age 74 days (Hunter, 1976). The most tenable explanation for this result is that it becomes physically impossible for larvae to ingest sufficient numbers of prey when the prey are below a certain size. To illustrate this point, I calculated the number of *Brachionus, Gymnodinium,* and *Artemia* needed for larvae of different sizes (Table 2). The calculation is based on oxygen consumption data of Lasker (unpublished data), and the caloric value for the different foods and does not include adjustments for success in feeding or digestive efficiency which would increase the numbers needed.

TABLE 2

Numbers of *Gymnodinium splendens*, *Brachionus pilicatilis* and *Artemia salina Nauplii* needed per day to meet metabolic requirements of anchovy of various sizes.

Larval length mm	Dry weight mg	Numbers needed per day *		
		Gymnodinium	*Brachionus*	*Artemia*
4	0.021	230	14	—
6	0.064	690	43	4
10	0.314	3,400	210	18
20	4.164	45,000	2,800	230

* Calculated from: A respiratory requirement of 0.54 cal/mg dry weight larval anchovy/day and the caloric value per organism of

Gymnodinium = 0.00005 cal

Brachionus = 0.0008 cal

Artemia = 0.0096 cal

These calculations indicate that extremely high rates of ingestion must be maintained just to meet metabolic needs when the prey is small relative to the larva. Feeding activity would be considerably higher than the required ingestion rate since feeding success and digestive efficiency is not 100%, and many feeding acts are not completed. Other works suggest that a prey too small to support growth alone still may be beneficial as a supplement to the diet as long as larger organisms are also available (Hunter, 1976).

From the above considerations it seems obvious that it would be adaptive for an anchovy larvae to select as large a prey as possible. Shirota (1970) correlated the gape of the mouth of various larvae to the width of typical foods and found reasonable correspondence between 50 to 75% of gape and the width of typical prey organisms. Ambiguity exists, however, on the critical dimension of prey. For example, Arthur (1956) used the maximum prey width when studying the food of anchovy larvae, whereas Berner (1959) used the maximum dimension. This is not a trivial point since copepods, the principal food of larval fishes, are oblong. Thus, to determine whether or not a copepod or a particular stage of copepod can be ingested one needs to know the critical dimension. To solve this problem and determine the relationship between feeding success and mouth size, the mouth size of larval anchovy was measured and compared to the feeding success of larvae fed freshly hatched *Artemia.* Anchovy larvae of various sizes were allowed to feed on *Artemia* nauplii (density 10 *Artemia* /ml), and their stomachs were examined 4 hours later. The larvae had no previous experience feeding on *Artemia.*

The mean size of the *Artemia* selected (0.236 mm wide x 0.433 mm long) was less than the mean size of the *Artemia* in the tank (0.260 x 0.525 mm). When the mouth width was equal to or less than the width of *Artemia* selected, no prey were taken, whereas, when the mouth was slightly larger than the width of *Artemia,* 25% of the larvae captured one or more *Artemia* (Figure 6). When the mouth size was 1.5 times the width of the prey (larval length 8.1 to 8.5 mm), all larvae ingested one or more *Artemia* in the 4 hour feeding period and the mean number eaten, 19 (N = 7), exceeded the numbers required to meet metabolic needs for an entire day. These results also indicate that all prey were ingested end on since the length of the *Artemia* exceeded the width of the mouth in all cases.

Thus, a reasonably close correspondence existed between the maximum width of prey that was ingested by larval anchovy and the width of the mouth. On the other hand, for ingestion of prey to be independent of mouth width, the width of the mouth must exceed that of the prey by about 1.5 times.

Estimates of Food Densities

Two approaches have been used to estimate the density of food needed for survival of larval anchovy. Survival can be determined for larvae reared in the laboratory at various food densities or alternately the required density can be calculated from a searching model based on estimates of daily ration and the volume of water searched by a larva per day.

O'Connell and Raymond (1970) using the first approach, determined that first feeding anchovy larvae need at least one copepod nauplius per ml to survive and four or more per ml to insure good survival (about 50% survival after 12 days at 17° C). Lasker (1975), in a series of density experiments, found that anchovy larvae need 20 to 40 *Gymnodinium splendens* cells/ml to fill their guts in 8 hours, and Lasker et al. (1970) found that 100 to 200 cells/ml were required to insure growth for the first week.

The searching model approach was employed by Hunter (1972) to estimate the food density requirements of anchovy larvae. The model is similar to models of Cushing and Harris (1973), Blaxter

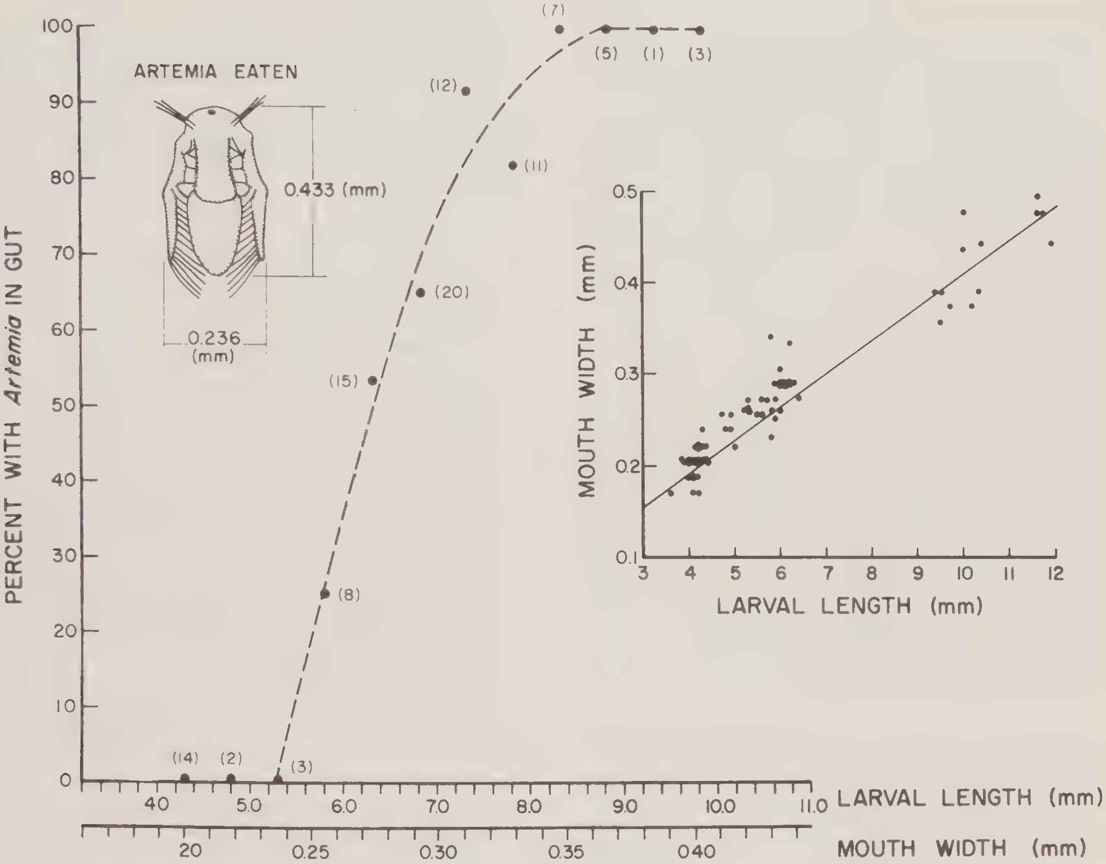

FIGURE 6. Percent of anchovy larvae with one or more *Artemia* nauplii in stomachs after 4 hours of feeding. Percentages calculated for 0.5 cm length classes and plotted at the midpoint of each class; number of larvae per class is given in parentheses. In the upper left corner the mean dimensions of the nauplii ingested are given, drawn to show the position of appendages when measured. Upper right, regression of mouth width (Y) on larval length (X) where Y = 0.0431 + 0.0366X and s_{yx} = 0.0585; this regression was used to construct mouth width scale at the bottom of the figure.

(1969), and Rosenthal and Hempel (1970). It is an estimate of daily ration, adjusted for feeding success, divided by the volume of water searched by a larva per day. The volume searched per day is the product of cruising speed (assumed here to be 0.29 cm/sec for a 4 mm larva) and the cross sectional area of the reactive perceptive field for prey (the attack range of Cushing and Harris, 1970). When the 95% limits of the perceptive field for prey are used (0.36 body length to the sides, and 0.40 body length above and below the swimming plane), the volume searched in 10 hours is 622 ml (Hunter, 1972). On the other hand, if the mean distance at which prey are sighted (0.185 body length) is used the volume searched per day is only 148 ml (data recalculated from Hunter, 1972). The ration is calculated from metabolic requirements for a 4 mm larva (Table 2), but is increased to account for digestive efficiency assumed here to be 80% (Lasker, 1965) and for feeding success which is 11% for first feeding larvae (Hunter, 1972). The ration adjusted in direct proportion to these percentages is 2,614 cells of *Gymnodinium.* Division of this ration by the two volume estimates gives 4 cells/ml when the 95% limits are used and 18 cells/ml when the average distance to prey is used. Despite the relatively large ration, the estimated densities are still below the densities of *Gymnodinium* required in laboratory tanks for larvae to survive.

The large difference between the estimate in which the mean perceptive field was used and the one in which the 95% limits was used, demonstrates the extreme sensitivity of the model to assumptions regarding the size of the perceptive field. Probably one of the more serious problems in models of this type is the tacit assumption that a larva reacts to and attempts to capture every prey that enters its perceptive field. In the laboratory, larvae frequently pass without responding to many *Gymnodinium* cells which appear to be in their perceptive field. It is likely that a larva reacts only to one prey at a time; thus, the division of the ration by the volume searched produces an unrealistically low food density requirement. The proportional increase in prey density to account for the prey attacked but not captured is probably also a source of error. In addition, search patterns of larval fish may have considerable redundancy (Hunter and Thomas, 1974). Clearly, more realistic models are required.

In summary, laboratory density experiments yield higher food density requirements for survival of anchovy larvae than simple searching models. The laboratory density experiments have the advantage that they measure density directly but they suffer from the possible existence of larval density dependent interactions, and a small tank volume which may limit the searching capacity of the larva. The searching model is not affected by these variables but is affected by errors in the parameters, and in the assumptions required by the model.

CONCLUSIONS

The average density of food in the sea is too low to support larval anchovy, regardless of whether one used laboratory density experiments or searching models. Lasker (1975) has recently shown that patches of dinoflagellates known to be nutritious to anchovy larvae exist in the sea in sufficient concentrations to support larval life during the first feeding stage. Laboratory studies reported here indicate that larvae have the ability to remain in patches of food once they find them. On the other hand, such patches may be ephemeral features, and even if they persisted for a reasonable period larvae would have to find other patches of larger prey to exist. Whether or not a larva will find a concentration of food organisms of the appropriate size and whether or not it will be able to survive until it finds another, involves a complex set of interacting variables including all of those described in this review. At present it is impossible to predict the outcome of such a series of interacting variables. Evaluation of this will require development of more complex models of larval feeding behavior and energetics than presently are available. I believe our understanding of the ecology of larval anchovy is at the point where such models could be constructed on a more realistic basis than has been possible in the past, and these models would expand our understanding of larval fish ecology.

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Welfare Implications of Extended U.S. Fisheries Jurisdiction
(Virgil J. Norton, University of Rhode Island, Chairperson)

Constraints to Welfare Gains under Extended Jurisdiction Fisheries Management

Daniel D. Huppert

The recent extension of the U.S. fishery conservation zone to 200 miles and the adoption of economic objectives for fisheries management in this zone make the consideration of welfare gains an important current issue. The economic objectives contained in the Fishery Conservation and Management Act of 1976 (FCMA) are especially noteworthy. It has been well established in both theory and practice that economic gains will not necessarily result from fishery management geared to the traditional biological objectives such as maximum sustainable physical yield (MSY). The maximization of social welfare requires the explicit consideration of economic values generated by fisheries, the private and social costs of exploiting and managing the fisheries, and the probable distribution of income resulting from fishery regulations. In addition, theoretical economic analyses must be tailored to statutory requirements and political necessities before economically sensible fisheries management will be achieved. To assure that this administrative and political process results in the realization of potential economic gains will be a long-term task for fisheries economists and administrators.

The received body of theory in fishery economics emphasizes the importance of free access to fisheries as a source of welfare loss. The theoretical argument has changed little since the publication of Gordon's seminal article in 1954. Gordon argues that a competitive industry exploiting a common property fish stock will grow until all potential net economic return (or rental value of the stock) is dissipated. Fishing vessels that are privately maximizing their own profits will fail to respond to the social costs of depleting the resource and, as a group, will deplete the fish stock until the average cost of production rises to equal the market price of the fish. If the rate of fishing were lower than the competitive equilibrium rate, the fish stock would be more abundant and the cost of production per ton of fish would be lower. The ideal economic solution to the common property (or "externality") problem requires that the investment of capital and labor in the fishery be prevented beyond the point where incremental costs are justified by marginal social returns. There are a variety of institutional arrangements that could facilitate the achievement of the economically efficient production pattern, including administrative allocation of fishing licenses, fixed price license sales, fishing license auctions, landings taxes, assignment of individual quotas to fishermen, and undoubtedly others (Christy).

The static economic efficiency theory has been extended to incorporate dynamic efficiency criteria by, for example, Brown and Clark. Also, numerous case studies have applied variations of Gordon's theory to real fishery situations and have uniformly found that efficient economic exploitation of fish stocks entails the maintenance of larger fish populations and smaller fishing fleets than would be achieved under free access competition (see, for example, Crutchfield and Zellner, Crutchfield and Pontecorvo, Gates and Norton, Huppert, or Bell). By maintaining smaller fishing fleets and larger average fish stock abundances, an efficient economic man-

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agement system would provide more real income to the nation than would either free competition or management for maximum physical yield.

Christy suggests that the total amount of economic yield lost through free access competition in the U.S. fisheries is on the order of $300 million annually. At 6% annual interest, the capitalized value of the lost economic yield is about $5 billion. This represents an impressive potential gain in real national income and should provide an incentive for greater efforts to achieve economic efficiency in fisheries.

Some Income Distribution Aspects

The body of traditional literature on fishery economics clearly emphasizes the inefficiency of free competition for fishery resources and prescribes economically efficient rates of exploitation. To a large extent, the policy prescriptions of received theory rely upon an implicit assumption that the group or groups subject to the welfare arguments are well defined. In actual fact, there are several stances that might be taken in defining the constituent group. Each definition carries with it a different set of conclusions for U.S. policy. Three possible accounting frameworks that come immediately to mind are (*a*) the group of existing participants in U.S. fisheries, i.e., the domestic fishermen; (*b*) the domestic populace as a whole, dominated by consumer interests; and (*c*) the world population. Clearly, the fishery management policies that would be adopted to benefit the existing domestic fishermen most would differ from the policies that most benefit the aggregate of domestic and foreign fishermen or that serve the population of the United States at the expense of foreign consumers and fishermen.

Although an interesting discussion could focus on the relative deservingness of foreign versus domestic interests, the FCMA is obviously intended to place U.S. citizens in a privileged position. However, maximizing domestic benefits from fishery resources in the Fishery Conservation Zone is not synonymous with developing a solely domestic fishery. Not only are some of the heavily exploited fishery resources presently utilized mainly by foreigners (such as Pacific hake and Alaska pollack) but it may well be that sunk investments in substantial vessel capacity coupled with lower wage rates make foreign exploitation an economically desirable alternative to development of domestic capacity.

Explicit economic cooperation is a growing possibility. Joint fishing arrangements between foreign interests and U.S. domestic companies are already beginning to appear. These arrangements take two forms: the foreign processing vessels plan to buy fresh fish from U.S. fishing vessels, and foreign companies invest directly in U.S. companies for the purpose of assuring a future supply of fish. In either case, the flow of fish from the U.S. zone to the foreign nation may proceed despite the declaration of exclusive fisheries jurisdiction by the United States. The United States can still benefit from the fishery harvests by harvesting and selling the fish, by participating in a joint venture to harvest and process the fish on U.S. soil before shipping to a foreign nation, or by simply charging a fair price for the foreign harvests.

Domestically, the welfare gain estimated by Christy could be distributed in a number of ways. If existing participants are freely given property rights to the annual yields of the domestic fish stocks and the exploitation of these stocks is rationalized through limited entry programs, the gain could accrue solely to the aggregate of fishermen. If, on the other hand, the marginal social value of the fish stocks is extracted from fishermen through taxes or license fees, the net economic value of fisheries could accrue through the public treasury to the U.S. populace as a whole. Innumerable combinations of fees and licensing arrangements could be devised to distribute any proportion of the potential economic value to both the fishermen specifically and to the public generally. In any case, the realization of the potential economic value is predicated on a reorganization of existing institutions. Such reorganization removes the long-observed right of all citizens to fish commercially and replaces it with a conditional permit to fish bestowed upon the chosen fishermen by the federal authorities. Regardless of how this transformation is engineered, some fishermen are bound to be excluded from traditional fisheries in order to allow the remaining participants (or the general public) to enjoy the fruits of economic efficiency. A measurable increase in net income to some existing and all future participants may not be socially desirable, however, if it is accomplished only at the cost of impoverishing some segment of the existing fishery or eliminating potential future income of yet unborn fishermen. Thus, the existing economic structure may combine with official reluctance to deal with difficult distributional issues and prevent the development of institutional arrangements that allow net economic benefit to be enjoyed from the nation's fisheries.

Potential Barriers to Welfare Gains

Because the FCMA provides the most important new set of institutions in the domestic fishery arena, most of my comments will focus on it. Nevertheless, the new fishery management councils and the Secretary of Commerce's authority to promulgate new fishery management regulations must be viewed as an additional layer of federal jurisdiction imposed upon established state/local and international institutions. States retain fishery management authority within their boundaries (i.e., within 3 miles of shore), and highly migratory species of fish, primarily tunas, remain within the institutional framework of international fishery management agreements. Also, many of the important species of fish exploited by U.S. fisheries do not obey the artificial political boundaries of the Fishery Conservation Zone. On the West Coast, transboundary stocks include the several species of salmon in the Pacific Northwest, the northern anchovy stock, and several commercially and recreationally important pelagic fish stocks. In the New England region, the major demersal fish stocks range significantly into the Canadian fishery zone. Superficially, the FCMA appears to create the mythical "sole owner" envisioned by Scott and other economic theorists, but in reality the federal authority created by the Act is but one of two or more authorities now claiming some management rights to many of the fish stocks important to the U.S. fishing industry.

The lack of comprehensive, unified management authority and the resulting possibility for counterproductive jurisdictional disputes can be identified as a significant institutional factor constraining the potential achievement of economic efficiency in U.S. fisheries. Disputes between state and federal authorities are likely to be of relatively minor significance due to the preeminence of the federal authority (sec. 306, FCMA). This is not to say that differences of opinion will be rare but only that the ability of the Secretary of Commerce to overrule state management regulations within state waters should be sufficient to prevent any substantial economic losses through inadequate management control in fisheries occurring both within state waters and the Fishery Conservation Zone.

In the international arena, of course, there is no similar superior authority. Ideally, the independent nations participating in a given fishery would reach agreement upon optimal management measures and would subsequently share in the economic benefits of efficient exploitation. In most cases, such agreement would probably have to rest upon improvements in the welfare of each participating nation. Crutchfield notes that most major international fisheries in the North Atlantic and North Pacific involve sufficient waste that rational management could provide adequate welfare gains to a large number of participating nations. Nevertheless, the institutions for implementing international management authority, even with unanimous agreement about its desirability, are either nonexistent or poorly organized in important cases. Also, it is unfortunately true that some nations may choose to engage in strategic behavior designed to gain them greater shares of the world's resources in the long run, rather than to join international agreements that tend to reinforce existing shares as a compromise position.

Although some nations may find unilateral or multilateral agreements beneficial even without full participation by all nations involved in the fishery, economic theory suggests that such actions may be disadvantageous. According to Anderson, if one nation reduces fishing effort in order to approach a unilateral optimum fishing level, there is an automatic incentive for other nations to increase their rates of fishing. It is even possible that the resulting decrease in available fish to the original nation could be of sufficient size that in the new international equilibrium the nation loses economically (Anderson). Under such circumstances, international cooperation would appear to be an all-or-nothing proposition. On the other hand, most shared fisheries important to the United States may be sufficiently controllable unilaterally to allow the achievement of some welfare gains without full international cooperation.

Some specific provisions of the FCMA and current implementing regulations may also act to retard progress towards economic efficiency. The FCMA specifically prohibits the Secretary of Commerce from collecting from domestic fishermen fees that exceed the administrative costs incurred in issuing permits to fish. This provision effectively bars any limited access program attempting to restrict fishing effort through imposition of user charges or attempting to extract some of the net economic yield from the fishing industry for support of scientific research, management costs, or general budget items. Without charging fees sufficiently high to extract rent or discourage excessive investments, a limited access program can still be implemented and can result in substantial economic efficiency benefits. But the distribution of the benefits is a rather nonnegotiable matter; the fishermen (or the owners of permits to fish, if not fishermen) will "get the swag." Depending on one's sense of distributive justice, this could be bad or good. But, as Christy observes, the general taxpayer will be footing the bill for research and management but not receiving any corresponding return from the public fishery resource, and the Office of Managenent and Budget may feel compelled to severely limit the funds for fisheries research and management.

The level of foreign fishing fees levied under the authority of section 204 of the FCMA is to be established by the Secretary of Commerce in consultation with the Secretary of State. The Act imposes no rigid limit on the fees charged to foreign interests, but the fees are to be reasonable and apply nondiscriminatorily to each nation. The fees adopted for the period starting 1 March 1977 include a permit fee of $1.00 per gross registered ton for each fishing vessel, $0.50 per gross registered ton for each processing vessel, and a flat $200 annual fee for each vessel assisting or aiding the fishing operation. Also, a poundage fee of 3.5% is levied against the exvessel value of the foreign harvests. As of 21 May 1977, nearly $10.3 million dollars had been collected from these fees—$785,087 in permit fees and $9.5 million in poundage fees. In adopting the fee schedule, the Department of Commerce decided not to use the fees as a management tool to restrict foreign fishing but did want to cover an appropriate part of the management costs related to foreign fishing. It was never made clear what the "appropriate part" of the costs were, but clearly the low poundage fee would not extract a significant portion of the total value of the foreign catch, estimated to be $271 million at 1977 prices.

The decision not to use the foreign fees as a management device or as a means to appropriate a significant part of the resource value has important ramifications. Under the constraint of minimal foreign fishing fees, the domestic optimization of fishery management may rely upon second-best measures, including an excessive emphasis on replacing foreign fleets with domestic fleets, even in those fisheries that are most efficiently prosecuted by foreign fleets. Also, some fisheries will continue to be dominated by foreign interests. In these, the combination of low fees and rationalized management could eventually result in a transfer of economic rents from the United States to foreign fishing firms. A theoretically sound fee structure would place a tax on harvests equal to marginal increase in fishing costs due to the reduction in fish stocks by harvesters (see Smith, p. 194, for example). While there may be compelling political and economic reasons for not charging such a tax to domestic fishermen, the extension of this policy to foreign interests will certainly reduce the welfare gains enjoyed by the U.S. citizens under extended jurisdiction fishery management.

Other possible constraints to the achievement of welfare gains arise from the regional orientation of the fishery councils and the makeup of the councils themselves. It seems highly probable that each Regional Fishery Management Council will tend to consider only regional income gains. Because the political and social, if not economic, importance of the regional fishing industry will loom larger than national concerns, a parochial view of management on the part of councils could easily lead to management plans aimed at improving the economic wealth of regional segments of the industry at the expense of the nation as a whole. Such a tendency could, for instance, be manifest in plans requiring tremendous inputs of research and administrative manpower, while requiring little or no restrictions on commercial fishing to improve efficiency and calling for no fees whatever to be paid by the beneficiaries of the plan.

Countering this tendency are the national objectives and standards of the FCMA. Specifically, the optimum yield of each fishery is to be defined such that the greatest overall benefit to the nation is served. Theoretically, such a yield is defined with a heavy weighting given to consumer interests, emphasizing larger sustainable supplies of fishery products and prices as low as possible under current cost structures. Also, the national standards relating to efficiency and cost minimization, if vigorously enforced by the Secretary of Commerce, would constrain the ability of Regional Fishery Management Councils to act in a nationally nonbeneficial manner.

One additional observation on the likelihood of fishery management being focused on local, rather than national, interests is appropriate. By and large, the appointed membership of the councils is dominated by industry spokesmen and others having long-time connections with past fisheries management bodies. While this is only natural under the circumstances, the new economic objectives and initiatives called for under the FCMA may not come easily from such management bodies. Experienced fisheries scientists and administrative officials in the United States have generally been reluctant to tackle issues of income distribution and economic efficiency. To many, limited access is anathema on ideological grounds. Witness the "Alaska limit" purse seiner, the sail-powered clam dredge, the grossly overcapitalized Pacific Northwest salmon fisheries. Combine this with the pronounced tendency of labor unions to maintain employment above technologically necessary levels, and the general interest of established industry members to protect entrenched interests, and there may be substantial resistance to the adoption of measures that improve fishing efficiency and that sufficiently reduce or retard overcapitalization.

A final constraint to improved economic performance of fishery management is the woefully inadequate existing economic knowledge of recreational fisheries and the consequent lack of serviceable economic models and measurements addressing the trade-offs between recreational and commercial fisheries. On a theoretical plane, enjoyment of fishing as recreation has as much claim to the attention of economic analysis as the consumption of fish as a commercial product. As a practical matter, the marine recreational activities have a substantial economic value. It should be expected, therefore, that a significant source of national welfare gain would accrue from optimal treatment of recreational fisheries.

One reason for the dearth of economic studies on recreation is the difficulty encountered in applying traditional competitive market theory. The output in the recreational fishery is not satisfactorily valued at market prices. Economists have emphasized that recreationalists are not buying fish but are paying for an experience, one aspect of which is the capture and consumption of fish. A commonly espoused institution in recreational fishing is free access to the resource.

Lacking adequate price data, demand curves can be estimated by the travel cost method (see Brown, Singh, and Castle) or the direct interview method (see Meyer). The resulting estimates provide a means of valuing fishing trips but do not necessarily yield information pertaining to the marginal value of fish to anglers. Special efforts must be made to estimate marginal values so that recreational and commercial values can be converted to the same economic units.

Further confounding the ability of fishery managers to adequately balance recreational and commercial values is the fact that the optimal yield and optimum stock size may be radically different for a recreational fishery than for a commercial fishery. As noted by Radovich, recreational fishing may be best with fish stocks much closer to virgin levels than to the level required for maximum sustainable yield. To the extent that a high catch-per-angler day is a valuable aspect of recreation, any attempt to optimize a commercial fishery will be of detriment to recreation. Also, large "trophy" fish are more abundant in a large, older fish population. Finally, there is some evidence that recreational fish have a greater tendency to strike angler's baited hooks when fish populations are closer to maximum abundance.

On the assumption that management authorities will take quantified, commercial value as more important than unquantified, recreational values for fish, the lack of established, measured values of fish to the recreational sector could result in substantial misallocations of fishery resources, reducing the welfare gain achieved under extended jurisdiction fishery management. The responsibility for solving this problem rests squarely on the academic and government economists involved in fisheries. The evaluation of all fishery sectors is, after all, the job of the practicing economists.

Conclusions

The fact that several important constraints to welfare gains can be found in current institutions should not be received with overwhelming pessimism. Necessary, but not sufficient, conditions for improved economic performance of U.S. fisheries are created by the passage of the Fishery Conservation and Management Act of 1976. Among these conditions are the establishment of federal authority over areas of sufficient breadth to allow unified management; creation of regional councils authorized to develop management plans with local industry cooperation as well as scientific advice; specific economic criteria for fishery management plans; and means to control foreign fishing harvests within the U.S. zone. Although there are some disturbing restrictions upon the use of economically desirable management tools (such as substantial fees or landings taxes on fishermen) and jurisdictional disputes could encourage economically inefficient fishery management plans, the success of the management effort to achieve economic welfare gains will depend more upon the actions and attitudes of the fishery councils and federal authorities than upon any rigid institutional constraints.

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Reprinted from
AMERICAN JOURNAL OF AGRICULTURAL ECONOMICS
Vol. 59, No. 5, December 1977

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Capture, Transportation, and Pumping of Threadfin Shad, *Dorosoma petenense*

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ABSTRACT

Methods of capturing, transporting, and acclimating threadfin shad, *Dorosoma petenense*, for use as live bait in skipjack tuna, *Katsuwonus pelamis*, fishing are described. The shad were captured in a 122-ha (302-acre) reservoir on Oahu Island, Hawaii, using a seine net either 146 or 110 m long and 7 m deep which was deployed from a skiff 6 m in length. Captured shad slowly swam to the shoreline while enclosed in a pocket of netting alongside the skiff. After being bucketed into 2,347-liter (620-gal) portable tanks, the shad were trucked 37 km to holding facilities at the Honolulu waterfront where they were acclimated to 100% seawater over a 72-h period. Up to 22,500 (40 to 70 mm long) shad in individual portable tanks have been trucked the 37 km distance with mortalities that on occasion have been less than 1%. Five experiments were conducted to determine the feasibility of pumping the shad with a vacuum pump and a centrifugal pump. Shad pumped were from 19 to 95 mm long in groups ranging from 1,210 to 1,633 individuals. Mortalities ranged from less than 0.1% 264 h after pumping to 9.7% 25 h after pumping. Use of the centrifugal pump is recommended.

INTRODUCTION

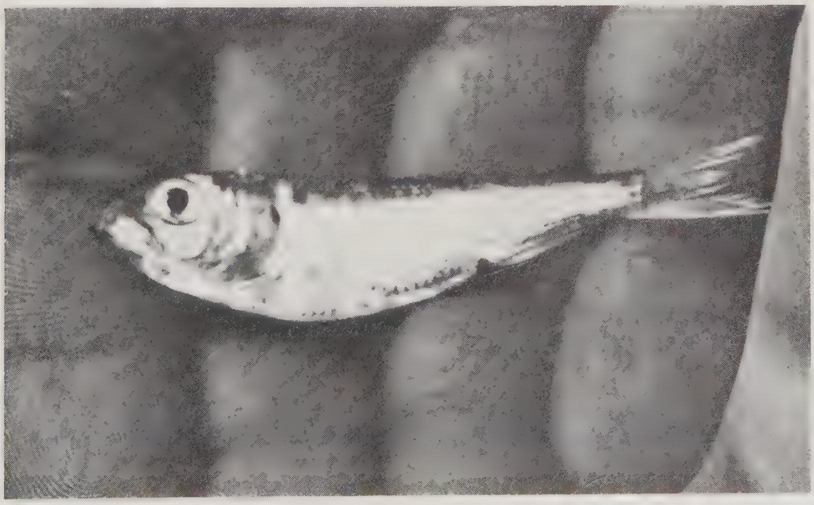
Development of an alternate live bait for Hawaii's pole-and-line fishery for skipjack tuna, *Katsuwonus pelamis*, by the Honolulu Laboratory, Southwest Fisheries Center, National Marine Fisheries Service, has since 1967 been based in part on the use of threadfin shad, *Dorosoma petenense* (Fig. 1).

In the process of capturing shad from a Hawaii reservoir, acclimating them to seawater, and conducting fishing trials, a considerable amount of experience has been acquired on handling and transportation of shad on a mass scale. The purpose of this report is to describe the techniques we have found successful in handling threadfin shad and also to present the results of several experiments which evaluated two different fish pumps for transferring shad.

SOURCE OF SHAD

Threadfin shad were first introduced into freshwater impoundments and streams in Hawaii in 1958, and by 1960 had become established in several reservoirs (Hida and Thomson 1962). Attributes of threadfin shad which

Figure 1.—Threadfin shad, *Dorosoma petenense*.



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[2] Bumble Bee Seafoods, Inc., Honolulu, HI 96809.

led to their investigation as a new baitfish are: tolerance to both freshwater and seawater, hardiness, silvery color, size, and swimming behavior. In recent years shad in Wahiawa Reservoir, Oahu, have become sufficiently abundant to make large-scale capture and fishing tests possible.

Wahiawa Reservoir is located in central Oahu, 37 km from the Honolulu waterfront, where they were trucked prior to experimental use. The reservoir has a surface area of 122 ha (302 acres) at high water, a maximum depth of 26 m, and contains approximately 1.14×10^{10} liters (3 billion gal) of water. The annual range in surface temperature is approximately 21°-30°C, and the annual fluctuation in water level can be as much as 12 m. Banks of the reservoir are as steep as 45° in many places; this allows the use of relatively deep seines close to shore where the shad often aggregate. The magnitude of the shad population in Wahiawa Reservoir is unknown but probably contains 14,000-17,000 buckets of shad during the summer (William Devick, Hawaii Division of Fish and Game, pers. commun.). During 32 days of baiting in the reservoir between 18 February 1970 and 16 August 1971, we captured 2,076 buckets of shad, an average of 65 buckets/day. More could have been captured, for the amount removed was limited by the carrying capacity of our portable tanks and the holding facilities at docksite. The unit of bait measure in the Hawaiian skipjack tuna fishery is the "bucket," so-called because the fishermen use stainless steel buckets to transfer the bait. A bucket of bait-sized (40-70 mm) shad weighs approximately 3 kg, ±1.5 kg, and contains about 1,500 shad, depending on size.

BAIT SEINE AND SKIFF

The principal seines used measured either 146 or 110 m long by 7 m deep. Side measurement of the square mesh was 6.4 mm. The longer net was set from a skiff 6 m in length, while the shorter net could be set from a 4.8-m skiff. The larger skiff contained a live well that could be used to transport a few buckets of shad to the truck when distance to the capture site was greater than about 0.5 km. A minimum of seven men were needed to set and haul either net, including two scuba divers.

PORTABLE TRANSPORT TANKS

Elliptical fiber glass tanks (Fig. 2) with a capacity of 2,347 liters (620 gal) were used to transport the shad. Each tank is 2.4 m long, 1.8 m wide, and 60 cm deep. An elliptical opening 46 cm wide, 76 cm long, with a raised 30 cm coaming, is located in the center of the lid. The lid is secured to the tank with wing nuts and bolts and can be removed. A detailed description of the tank, base, and lifting A-frame is given by Nakamura (1966). These tanks were originally designed for the transfer of tuna and other pelagic fishes to shoreside tanks. A 7.5-cm-diameter drain pipe is located in the bottom of the tank. We later added a plastic cloth tube 30 cm in diameter by 1.1 m long to the other end of the tank. This allowed rapid transfer of the shad with less crowding in the tank as the water level dropped. The entire tank could be drained in 60 s through this tube. When not in use, the tube was rolled up and held tightly against the outside wall of the tank by a hinged aluminum cover (Fig. 3).

OXYGENATION SYSTEM

The oxygenation system consisted of a 6.8-m^3 cylinder of 100% oxygen, pressure regulator, a 10-gang valve, and hoses leading to two oxygenation stones in each tank (Fig. 4). The oxygenation stones were modified from grinding wheels (#800 grit) 15 cm in diameter. The upper and lower surfaces of the grinding wheels were coated with fiber glass resin and the oxygen bubbles escaped from the outer edges of the stones. Such oxygenation devices release bubbles about 0.25 mm in diameter and are much more efficient than round aquarium stones which release much larger bubbles. For a description of this type of an oxygenation device, see Baldwin 1970.

DOCKSITE HOLDING TANKS

Circular, plastic-lined swimming pools, 7 m in diameter and 1.2 m deep, containing 34,822 liters (9,200

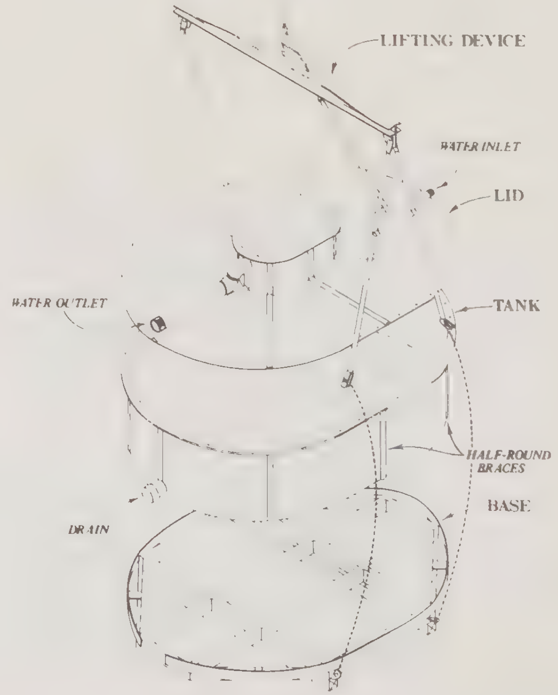

Figure 2.—A diagram of the portable transport tank, base, and lifting device. From Nakamura (1966).

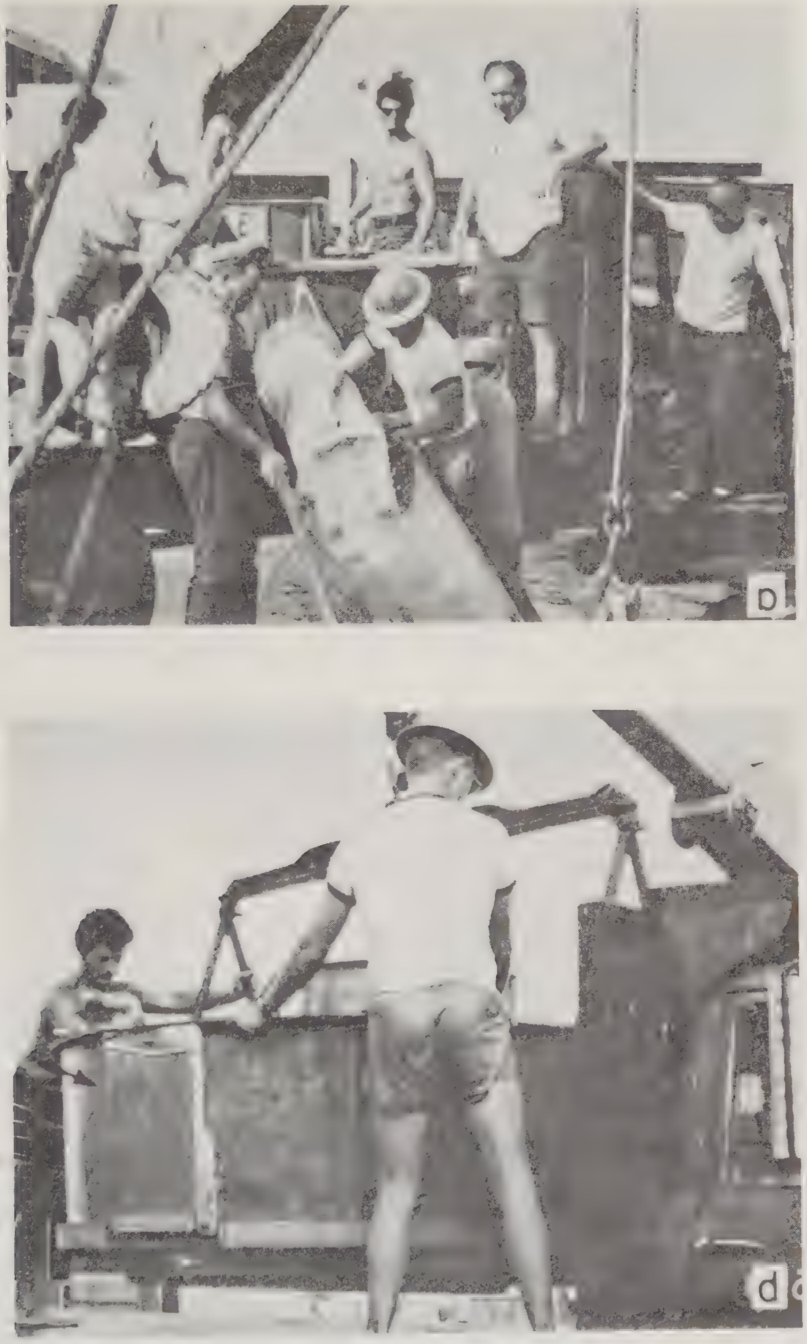

Figure 3.—(a) Plastic cloth tube attached to portable transport tank for rapid unloading of baitfish. (b) Hinged aluminum cover holding rolled up tube against outside of tank (arrow).

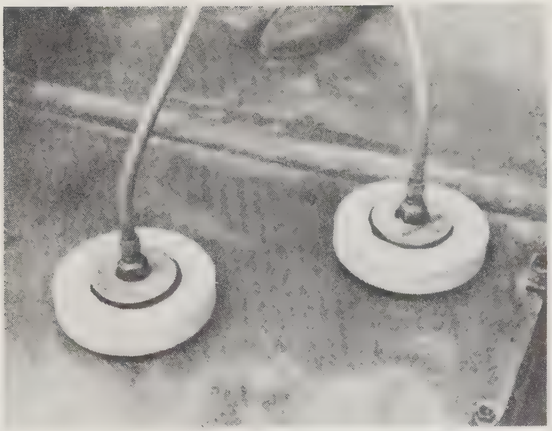

Figure 4.—Oxygenation stones used during transportation of shad. They are modified from 15-cm-diameter grinding wheels.

gal) of water, were used to hold the shad during acclimation to seawater (Magnuson 1965).

FISH PUMPS

Two pumps were tested. One, the Morton[3] batch pump developed by the Oregon State Game Commission (Morton 1963), utilized a vacuum principle to move the shad. The other was a standard centrifugal pump used extensively in the food processing industry.

Morton Batch Pump

This device (Fig. 5) is operated on a vacuum principle with a 76.2-mm (3-in) Homelite 1,135 liters/min (300 gal/min) water pump. A 5.2-m snorkel tube, 12.7 cm in diameter, is attached to the top of a fiber glass vacuum tank holding approximately 946 liters (250 gal) of water. The other end of the snorkel tube is submerged in the holding tank. The system is pumped full of water and all air purged from the system by a valve on the top of the vacuum tank. The water flow is then reversed instantaneously by closing two three-way valves. As the water is drawn from the vacuum tank through the bottom, the fish are gently drawn into the tank via the snorkel tube in the holding tank. After the fish enter the vacuum tank, the vacuum is broken by the air-purge valve and the water flow reversed. The end of the snorkel tube is then raised to the receiving tank and the water flow increased. A round brass screen crowder in the bottom of the vacuum tank is slowly raised to the top of the tank, gently forcing the fish into the snorkel tube for delivery to the receiving tank. The screen crowder is then lowered to the bottom of the vacuum tank before the next "batch" of fish enters the tank.

Centrifugal Pump

This system (Fig. 6) consisted of a Pacific Pumping Company 10.2 cm (4 in) BM type standard frame mounted food pump, and a Reliance 3 hp variable speed

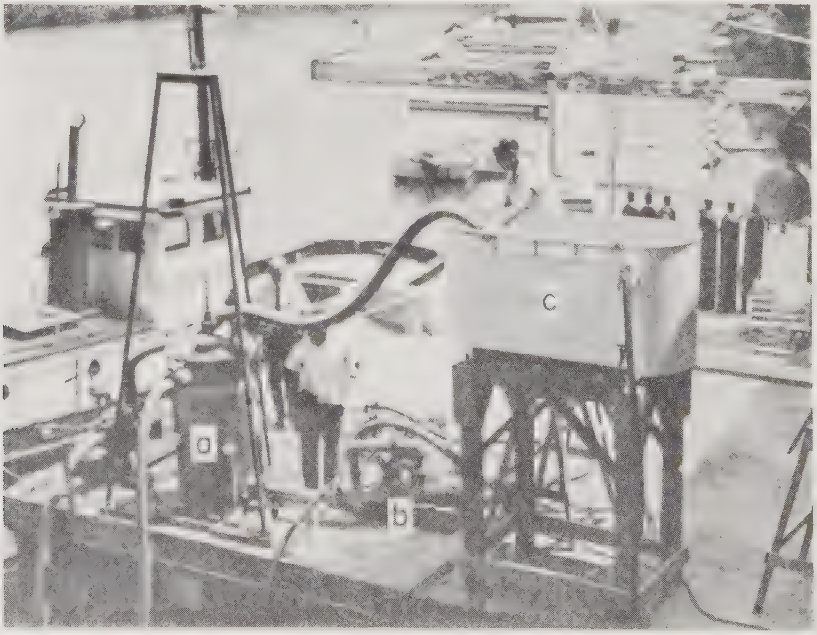

Figure 5.—Morton batch pump system.
(a) Fiber glass vacuum tank.
(b) Pump and motor.
(c) Elevated receiving tank.
(Hawaii Institute of Marine Biology photo.)

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[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

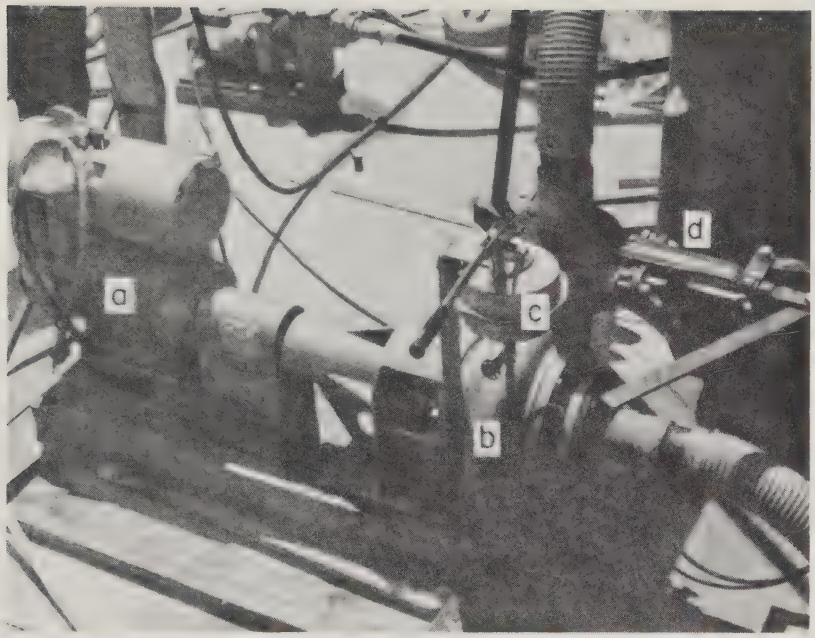

Figure 6.—Centrifugal pump.
(a) Motor. (c) Printing unit.
(b) Pump. (d) Fabri valve.
(Hawaii Institute of Marine Biology photo.)

drive electric motor (600-1,200 rpm). Other components were a 10.2-cm (4-in) Fabri valve and a 12.7-mm (½-in) hand-operated diaphragm priming unit. Smooth bore plastic hose, 10.2-cm diamter, was used on the suction and discharge sides of the pump. This pump has a hollow impeller and the fish pass through the impeller as they move through the pump.

CAPTURE AND HANDLING

Seining

Upon locating a school of shad, the seine was set in a large circle around the school. Some sets were "blind" sets, i.e., sets made with no surface signs of shad. After completion of a set, the ends of the float line were draped over the bow and stern of the skiff, and the ends of the lead line were brought together amidships. One swimmer was positioned at the water's surface next to the skiff to keep the two lead lines close together, and as far as possible, in a vertical position. Two other swimmers using scuba gear were positioned 4.6 to 6.1 m (15-20 ft) below the surface swimmer in order to keep the lead lines together and prevent an opening under the boat through which the shad might escape. In case of snags on bottom debris, one scuba diver could patrol the lead line until the obstruction was cleared. The scuba divers also assisted in pulling the net while underwater.

One end of the net was then hauled until the entire lead line was aboard, and a small pocket of netting was formed alongside the skiff. Bamboo poles and oars were used to keep the pocket from collapsing, and the shad in the pocket were slowly brought to the shoreline with the outboard motor at slow speed (Fig. 7). As much as 128 buckets of shad per set have been captured and delivered to the shoreline in this manner. Times en route after the shad were in the pocket have been as much as 30 min. Upon reaching the shoreline, the floaters of the net were placed over the edge of a floating dock which had one arm extending from each end in order to keep the skiff about 1 m (Fig. 8) from the dock. This prevented the pocket in the net from collapsing. The net was then gradually gathered up and the concentrated shad were bucketed (Fig. 9) to the portable transport tanks on the trailer (Fig. 10). Other species were often captured with the shad, especially *Tilapia* sp., and catches of 25 to 50 kg of tilapia per set were not uncommon. Some tilapia escaped by jumping over the float line (Fig. 7) while others were removed by using a large mesh (5-7 cm) dip net to separate them from the shad. The distance over which the shad were carried in the buckets was not less than about 10 m and occasionally was as much as 40 m.

Transportation[4]

Ten to fifteen buckets of shad were usually placed in each portable tank for the 37-km trip to the docksite, but on two occasions 21 to 27 buckets per tank were carried with mortalities of only 1% or 2%. We carried five por-

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[4] This report does not cover experiments in transporting shad during 1975 utilizing a 18,925-liter (5,000-gal) tanker-trailer. A total of 1,241 buckets of shad were captured during 25 days of baiting from 23 June to 18 September 1975. Mortalities during the transport phase were low, less than 10%, but became heavy during the acclimation phase, probably due to excessive handling as the fish were removed from the tanker-trailer.

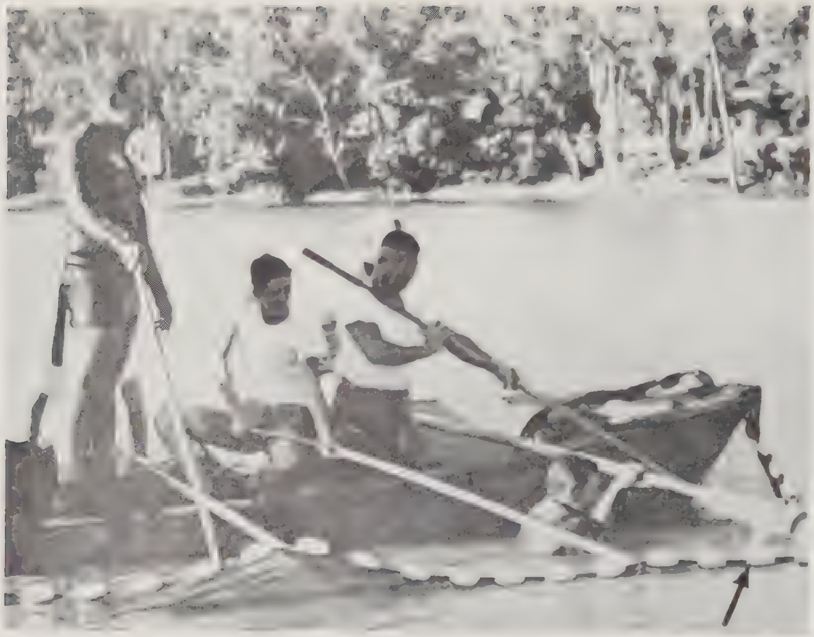

Figure 7.—Delivering threadfin shad to shore via net. Note the tilapia (arrow) escaping by jumping over the oar and float line.

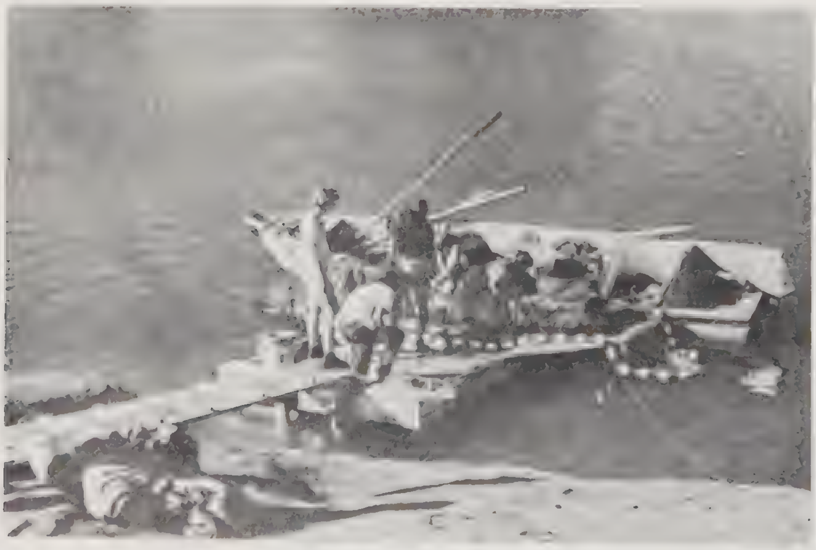

Figure 8.—Floating dock used in removing shad from the bait seine.

table tanks on a 12.2-m-long (40-ft) flatbed trailer (Fig. 10). Water in the tanks was a mixture of 75% freshwater and 25% seawater, and was not recirculated. Seawater was added to make the transport water more closely isotonic with the shad's internal environment, thus lessening osmotic stress caused by loss of scales during capture and bucketing. Tranquilizing chemicals were not added to the water.

An oxygen level of at least 10 ppm was maintained in the portable tanks, and levels that occasionally reached as high as 17 ppm for a short time did not have any adverse effect on the shad. Oxygen levels were checked about every 30 min with a portable electronic oxygen meter. Under these conditions it was not unusual to find less than 100 dead shad out of 15 buckets (ca. 22,500 individuals) in a portable tank upon arrival at docksite.

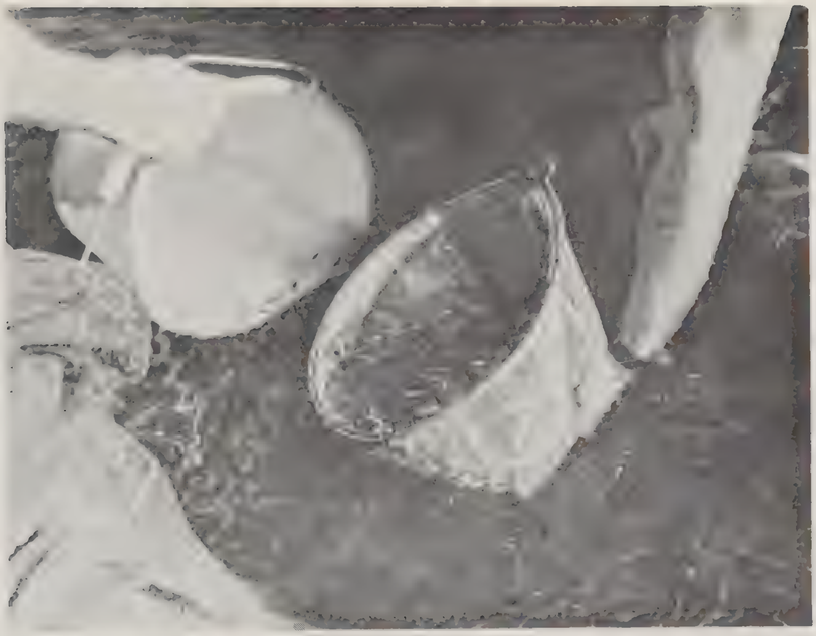

Figure 9.—Bucketing shad from the bait seine. Note adequate supply of water in the bucket.

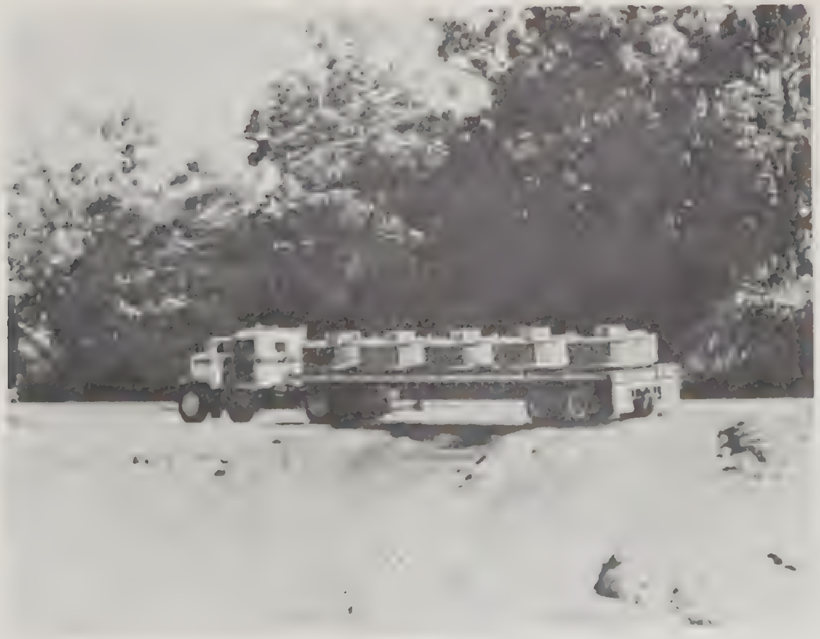

Figure 10.—Portable tanks and trailer used for transporting shad.

On a few occasions we had no mortalities. If the oxygen level went as low as 3 ppm, even momentarily, mortalities as high as 50% sometimes resulted. High oxygen levels are apparently required to offset an oxygen deficit incurred during capture and bucketing.

Upon arrival at docksite, the shad were transferred to the large holding tanks either by immersing the portable tank, minus the lid, and then overturning it (Fig. 11) or through the plastic cloth tube (Fig. 12). Immersing the portable tank resulted in fewer mortalities.

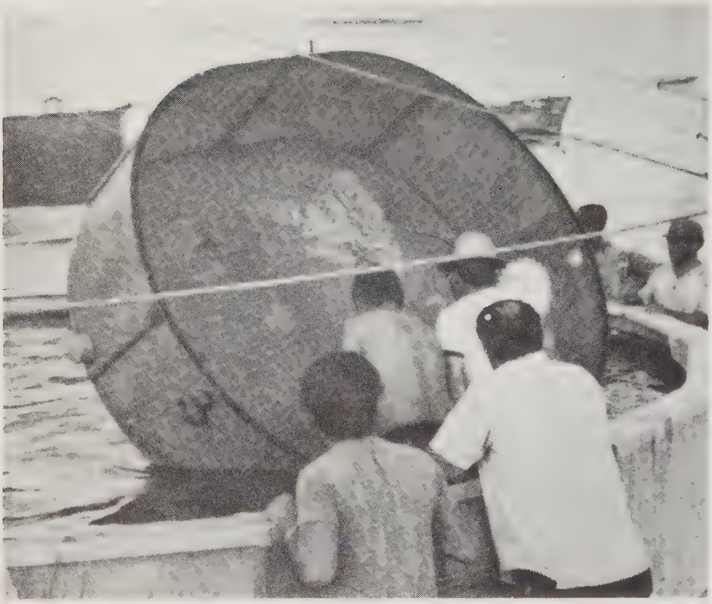

Figure 11.—Overturning a portable transport tank to transfer threadfin shad to the 34,822-liter (9,200-gal) holding tank for acclimation to seawater.

Acclimating Shad to Seawater

We have found it possible to acclimate shad from freshwater to seawater in 8 h, using shad held in captivity for 2 mo. However, we ordinarily took from 36 to 72 h, preferably 72 h, to acclimate them if the acclimation period occurred just after capture. For a 72-h acclimation period the shad were held in 75% freshwater and 25% seawater for the first 24 h; 50% freshwater and 50% seawater for the next 24 h; 25% freshwater and 75% seawater for the next 24 h. Following this time the freshwater was turned off over a period of several hours. Through trial and error, we have found it impractical to acclimate more than about 50 buckets of shad in a 7-m diameter tank with 34,822 liters (9,200 gal) of water. The flow of water into such a tank should not be less than 284 liters (75 gal)/min, and preferably 378 liters (100 gal)/min. Once the shad are in large holding tanks, the oxygen level should not be less than 5 to 6 ppm. We did not recirculate the water supplying the large holding tanks. When possible, shad were held for several days in 100% seawater prior to placing them aboard vessels for fishing. The best sign of shad in good enough condition to withstand the rigors of a second transfer to a fishing vessel's baitwell is a tank of actively feeding fish. We used a mixture of 50% fish meal and 50% trout chow to feed the shad.

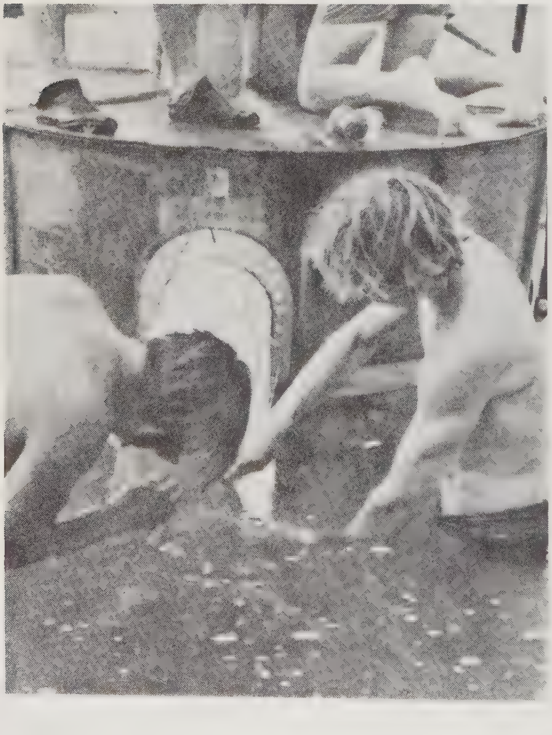

Figure 12.—Plastic cloth tube extending from portable transport tank. The tube is used to flume shad from the portable tank into a larger shad holding tank. The portable tank is partially immersed in the large holding tank.

Transfer of Shad to Vessels

Shad were transferred to the fishing vessel either by bucketing or by the portable tank used to transport the shad from the reservoir. A small crowder was used to concentrate the shad for bucketing or for herding into the submerged portable tanks. Bait was drained from the portable tank into the vessel's baitwells by two methods. One method employed a smooth bore plastic hose 10 cm in diameter placed over the 7.5-cm drain pipe. The tank was then lifted by crane, and the bait flowed through the hose into the baitwell. One man was deployed on top of the tank with a seawater hose to flush out the last of the shad and to provide enough weight to tilt the tank slightly. Using this technique, for example, 113 buckets of shad were transferred by hose into three baitwells of the RV *Charles H. Gilbert* during cruise 116 with a mortality of only 2% the following day.

The other draining method employed the large diameter plastic cloth tube and long stainless steel chutes (Fig. 3) to place bait aboard the purse seiner *Jeanne Lynn*. Mortalities aboard the *Jeanne Lynn* averaged 10% for six transfers. Until 1971, over a wide variety of transfer conditions to different vessels, the average mortality of 1,033 buckets of shad the following day was 16%. In some cases, it was necessary to bucket the shad under adverse conditions, or to place shad aboard that had not been completely "rested" following acclimation to seawater. Assuming optimum conditions for transfer, we believe mortalities of 10% or less can be consistently achieved. This is suggested by the fact that placing 204 buckets of shad aboard the fishing vessel *Marlin* during July and August 1971 for commercial fishing trials resulted in a mortality of only 7%. Once shad have adjusted to the baitwell environment, long distance transportation at sea is feasible. The 113 buckets aboard the *Gilbert* during cruise 116 were carried for 14 days to an area 4,300 km southeast of Hawaii for use as live bait in skipjack tuna fishing. Mortalities of these shad en route were negligible.

We placed up to 36 buckets of shad aboard the *Gilbert* in a baitwell containing 10,704 liters (2,828 gal) of water, for a maximum ratio of one bucket of shad per 295 liters (78 gal) of water. Water flow through the baitwell was 378 liters (100 gal)/min. This is less than the ratio of one bucket of shad per 696 liters (184 gal) of water for 50 buckets of shad in 34,822 liters (9,200 gal) of water in the holding tank. When 36 buckets of shad were placed in the baitwell, the mortality was 7% for the first 24 h. On a few occasions when shad were placed aboard commercial skipjack tuna vessels, the maximum crowding ratio was one bucket per 322 liters (85 gal) of water.

PUMPING EXPERIMENTS

During the summer of 1970, the purse seiner *Jeanne Lynn* was chartered by Bumble Bee Seafoods, in a joint venture with the State of Hawaii, to conduct experimental purse seining for skipjack tuna in Hawaiian waters ([Hawaii.] Division of Fish and Game and Bumble Bee Seafoods [1970]. In anticipation of the need to use live bait in conjunction with purse seining, several experiments were conducted during August 1969, to test the feasibility of pumping shad from a portable transport tank to a 1,260-liter (333-gal) receiving tank elevated 3 m above the portable transport tank. The tests simulated pumping bait from the *Jeanne Lynn*'s baitwell to a bait skiff on the deck above.

Following capture, the threadfin shad used in the experiment were acclimated to seawater in the portable transfer tanks instead of the large holding tanks. Water flow through the portable transport tanks was 19 liters (5 gal)/min. An oxygen level greater than 5.0 ppm was maintained by bubbling compressed air through three airstones. Water flow through the elevated receiving tank was 8 liters (2 gal)/min and oxygen was provided in the same manner as the portable transport tanks. The shad were acclimated to seawater over a 48-h period. The shad used for the tests ranged from 13 to 95 mm total length. Mortalities were computed by weight as well as by number.

About 3 to 5 buckets of shad remained in the tanks upon completion of acclimation, but only one to two buckets were pumped during any one experiment. Water temperature in the portable tanks and elevated receiving tank was 24° to 26°C.

After pumping, the dead bait were removed every hour or several hours for the first 4 to 8 h, counted, and weighed. The remainder were left unattended overnight. The following day the dead fish were removed, counted, and weighed. The tank was then drained and the remaining fish were counted and weighed. A screen on the drainpipe prevented the loss of shad between measurement intervals.

Mortalities in the hours following pumping for the five tests are given in Table 1. Mortalities for shad pumped with the centrifugal pump ranged from less than 0.1% by number and weight after 11 days to a high of 5.0% by weight and 9.7% after 25 h. Mortalities of the shad pumped through the batch pump were intermediate. The low mortalities observed during centrifugal pump tests 2 and 3 are apparently due to larger average size of the shad used for these tests. However, the mortalities observed with the smaller shad are still much less than those occurring during the first 24 h with the nehu, *Stolephorus purpureus*, used as skipjack tuna bait by Hawaiian fishermen. The average mortality of nehu for the first day after capture is about 25% (Brock and Uchida 1968).

No significant difference is apparent in mortalities between the two pumps. However, since the batch pump is more difficult to operate, and pumping times are twice as long, the centrifugal pump is recommended for pumping threadfin shad. Care should be taken, however, that all internal surfaces of the pump and impeller are smooth and free of holes. Two preliminary tests when the centrifugal pump had a hole in the impeller resulted in mortalities of 75% to 90% within 5 min after pumping. After the impeller was repaired, rust removed, and the inside of the pump painted, the results cited above were obtained.

ACKNOWLEDGMENTS

We thank Wayne J. Baldwin, Randolph K. C. Chang, Roger E. Green, and Eugene L. Nakamura for reading

Table 1.—Mortalities of threadfin shad after pumping.

Test No.	Date 1969	Total length		Quantity pumped		Pumping time (min)	Mortalities		
		Range (mm)	Mean (mm)	(no.)	(g)		Elapsed time (h)	Cumulative percent	
								(g)	(no.)
Morton batch pump									
1	8/13	19-51	38	1,348	2,035.2	10	1	0.5	0.7
							2	1.0	1.4
							4	1.9	2.4
							5	2.9	3.7
							7	3.6	4.8
							23	4.6	6.2
2	8/14	51-64	—	1,210	2,960.4	11	1	1.6	1.3
							5	1.9	1.8
							22	2.1	2.0
Centrifugal pump									
1	8/22	13-38	—	1,257	1,699.1	3	1	1.2	2.6
							2	2.3	4.2
							3	2.9	6.0
							5	3.6	7.2
							25	5.0	9.7
2	8/28	19-95	64	1,633	2,629.1	4	1	0.0	0.0
							2	0.0	0.0
							4	0.0	0.0
							8	0.0	0.0
							23	0.1	< 0.1
3	8/29	19-95	64	1,511	2,908.1	5	1	0.0	0.0
							2	0.0	0.0
							4	0.0	0.0
							8	0.0	0.0
							24	0.0	0.0
							264	< 0.1	< 0.1

the manuscript and for technical advice. We also thank the many crewmen, technicians, and biologists of the Honolulu Laboratory, NMFS, for their efforts in catching and transporting the shad. The pumps were provided through the courtesy of Bumble Bee Seafoods and the Oregon State Game Commission.

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Use of Marine Meteorological Observations in Fishery Research and Management

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Gunter R. Seckel, Chief, Pacific Environmental Group
National Marine Fisheries Service

Resource Category	Potential Increase (millions of tons) 1985	2000
Conventional species	8	14
Unconventional species (krill, squid, etc.)	5	35
Waste elimination (equivalents)	2	15
Total	15	64

Table 1. Opportunities for increased fish and shellfish production, 1985 and 2000 (Alverson, 1975)

Introduction

During the last 20 years there has been a phenomenal growth in world fisheries. Catches (marine and freshwater) rose from 27.6 million metric tons in 1954 to a peak of 70.2 million metric tons in 1971. The collapse of the Peruvian anchoveta fishery caused the subsequent decline to about 65 million metric tons in 1972. The anchoveta catch declined from a peak of 12 million to 2 million metric tons in 1973. This decline was probably caused by a combination of over-fishing and adverse environmental conditions, specifically, the occurrence of El Niño, a weather-related ocean change that visits the coast of Peru at irregular intervals.

Despite the leveling off of the total catch since 1970, there remains opportunity for significant further increases in the supply of protein from the sea. In summarizing the various possibilities, Alverson (1975) estimates that production from the ocean alone could rise from 55 million metric tons in 1973 to about 119 million by the year 2000, an increase of 64 million tons (table 1).

In a world desperately in need of protein, the possibility for increasing marine production cannot be ignored. However, this possibility will be realized only by better management of fishable stocks. Clearly, the collapse of the Peruvian anchoveta fishery points out the need for more efficient fishery management and increased research to better understand the effects of environmental changes on living marine resources.

Despite the large amount of environmental data collected over the past several years in fishery research programs, the most useful information is the marine surface meteorological observations and their historical record. There is no other marine data set that is global in nature and covers such a long period of time. These attributes are precisely what is needed in many kinds of environment-related fishery research.

Relationships established between environmental changes and fish stocks usually are empirical, and the cause-and-effect relationships may not be well understood. Thus, it is possible that the decline in a fishery is due primarily to fishing efforts too heavy for the fish stock to sustain, and the apparent relation to environmental change is only coincidental. The emerging consensus appears to be, however, that declines in many exploited fish stocks are caused by a combination of adverse environmental conditions and heavy fishing pressure. In the following examples we illustrate relationships between changes in some fisheries and environmental indices. The indices were derived from marine surface meteorological observations.

Salmon

A climatic shift occurred in the Bering Sea in the early 1970's which has had a drastic effect on the Alaska salmon fishery and significant effects on other fisheries. The 1973 and 1974 commercial salmon harvests were among the lowest since inception of the salmon fishery in the late 1800's. The low catches are attributed to the effect of the unusually cold years of 1971 and 1972 in the Bering Sea. Ocean sea surface temperatures near the Aleutian Islands in these years were the coldest for at least twenty years. In the winter of 1970-71, Aleutian land stations reported all-time low temperature readings.

The onset in the decline of sea and air temperatures appeared to coincide with an unusual southward penetration of the Arctic ice pack (Kukla and Kukla 1974). Using marine surface meteorological data, McLain and Favorite (1975) related the cold sea temperatures to large changes in North Pacific atmospheric circulation. These changes, producing northerly winds over the eastern Bering Sea, probably displaced the ice pack southward. Severe environmental stresses may have affected salmon survival in all phases of its life history, i.e., in lakes, streams, and the ocean. The severe conditions in the first two habitats appear to have been the cause of most mortality.

Atlantic Menhaden

The Atlantic menhaden at one time constituted the largest U.S. fishery. Recent studies concerning the size of yearly broods in this fishery suggest that annual variations in the surface water drift during the egg and larval stages may have been the predominant cause of variations in year-class size.

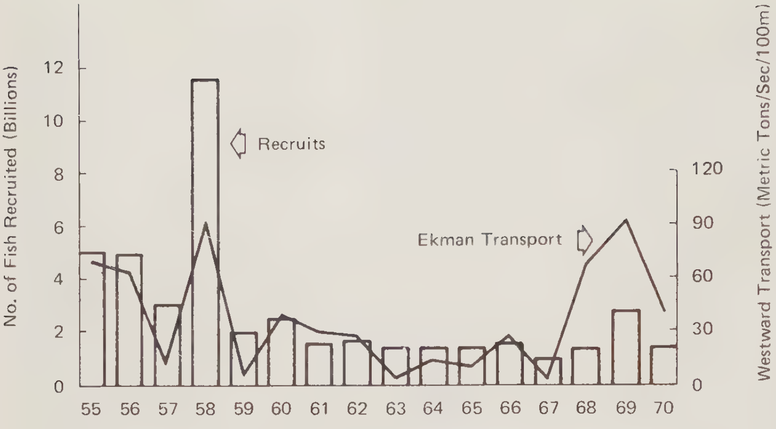


Fig. 1

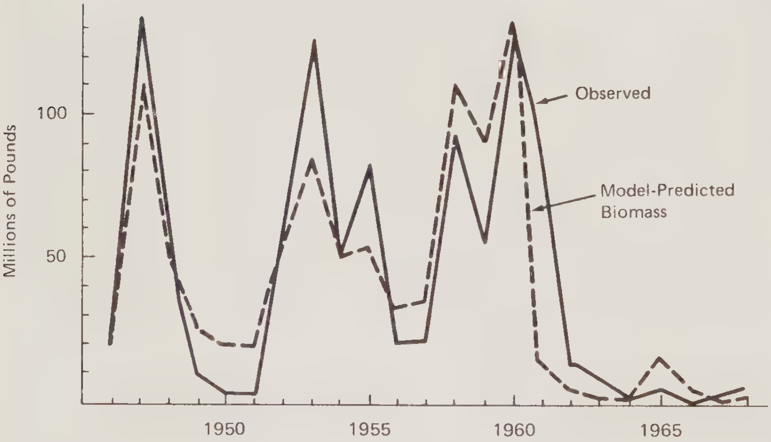


Fig. 2

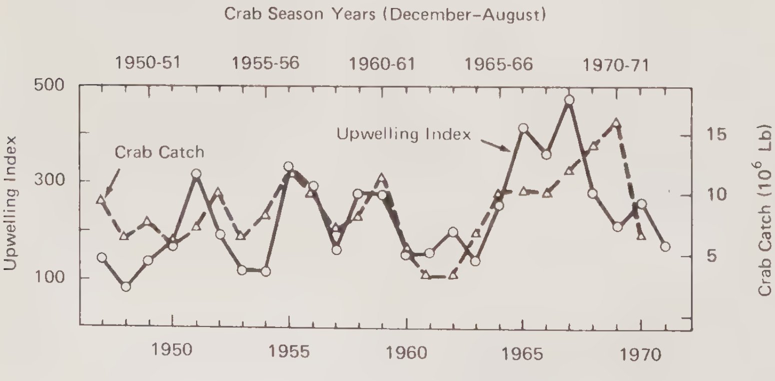


Fig. 3

The composition of the Atlantic menhaden stock obtained yearly since 1955 shows a range in number recruited into the fishery of from 11.5 billion in 1958 to 0.9 billion in 1967. Although some variation in recruitment can be attributed to fluctuation in the size of the spawning stock, Nelson, Ingham, and Schaaf (1976) found that much of this wide range in year-class size was related to an index of surface water drift. Marine surface meteorological observations (wind and atmospheric pressure) were used to calculate an index of surface water drift, commonly called Ekman drift or transport (Bakun, 1973). Figure 1 illustrates the relationship between the magnitude of the westward or onshore drift and the year-class size. The relationship is interpreted to mean that westward surface wind drift favors drift of eggs and larvae from the ocean spawning grounds to the estuarine environment which favors menhaden survival.

Pacific Mackerel

The California fishery for Pacific mackerel is another example of environmental variation during the egg and larval stages affecting the success of the fishery. Fluctuations in year-class size were large before the demise of this fishery in the late 1960's (fig. 2). Parrish (1976) showed that most of the variation

Fig. 1. *Atlantic menhaden recruits at age one and east-to-west Ekman transport. (Nelson, Ingham, and Schaaf, 1976.)*

Fig. 2. *Year-class size in the California stock of Pacific mackeral. (Parrish, 1976.)*

Fig. 3. *Upwelling index values versus crab catch in Oregon. Catch lags upwelling by 1.5 years (Peterson, 1973).*

in year-class size and, thus, the size of the later fishable population, was related to fluctuations of upwelling and surface water convergence in the spawning grounds of the mackerel. In addition to the observed year-class size, figure 2 also shows the predicted year-class size in a simulation model using these environmental indices. Several years of unfavorable environmental conditions occurring during a period of increased fishing pressure caused the demise of the fishery. Population simulations suggest that the fishery would have partially recovered in the early 1970's if the effect of the environmental conditions had been recognized in time to reduce the fishing pressure before the collapse occurred. Again, indices of upwelling and surface water convergence were calculated from marine surface wind and atmospheric pressure observations (Bakun and Nelson, 1975).

Dungeness Crab

An empirical relationship between the success of the valuable crab fishery off the U.S. west coast and intensity of upwelling has been indicated by Peterson (1973) and Botsford and Wickham (1975). The upwelling index again is that calculated by Bakun (1973) from marine surface observations. The relationship for the period 1948 to 1975 is shown in figure 3, with the crab catch lagging the upwelling index by 1.5 years. The relationship is holding for recent years not shown in the figure. There was anomalously intense upwelling off Northern California in 1974, 1975, and 1976, accompanied by rising crab landings. The 1974-75 landings increased by a factor of more than four, and the 1975-76 landings increased by a factor of more than thirty over the low landings of the 1973-74 season.

Currents and Fish Distributions

Another type of environment-

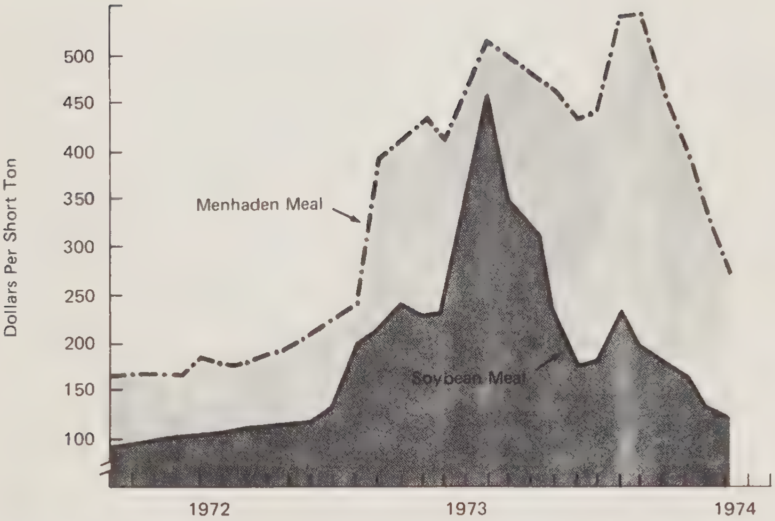


Fig. 4. Changes in monthly prices of menhaden and soybean meal.

fishery relationship concerns ocean currents. Currents can determine the migration paths of fish, as well as concentrate or disperse fish, and so affect their availability to the fisherman. For example, skipjack tuna that are found off Baja California appear one to two years later in the Hawaiian fishery. Seckel (1972) modeled the effect of baroclinic flow and surface wind drift on floating objects that had been distributed meridionally at longitude 120°W. After about two years, these objects were distributed zonally near Hawaii. Marine surface observations were used to calculate the wind-driven surface flow. The work of Meyers (1975) indicated that, in time, it may be possible to use surface observations to estimate the seasonal variability in the baroclinic flow of the Pacific North Equatorial Current. This means that the effect of currents on fish migration can be simulated by using marine surface observations.

El Niño and Air/Sea Interactions

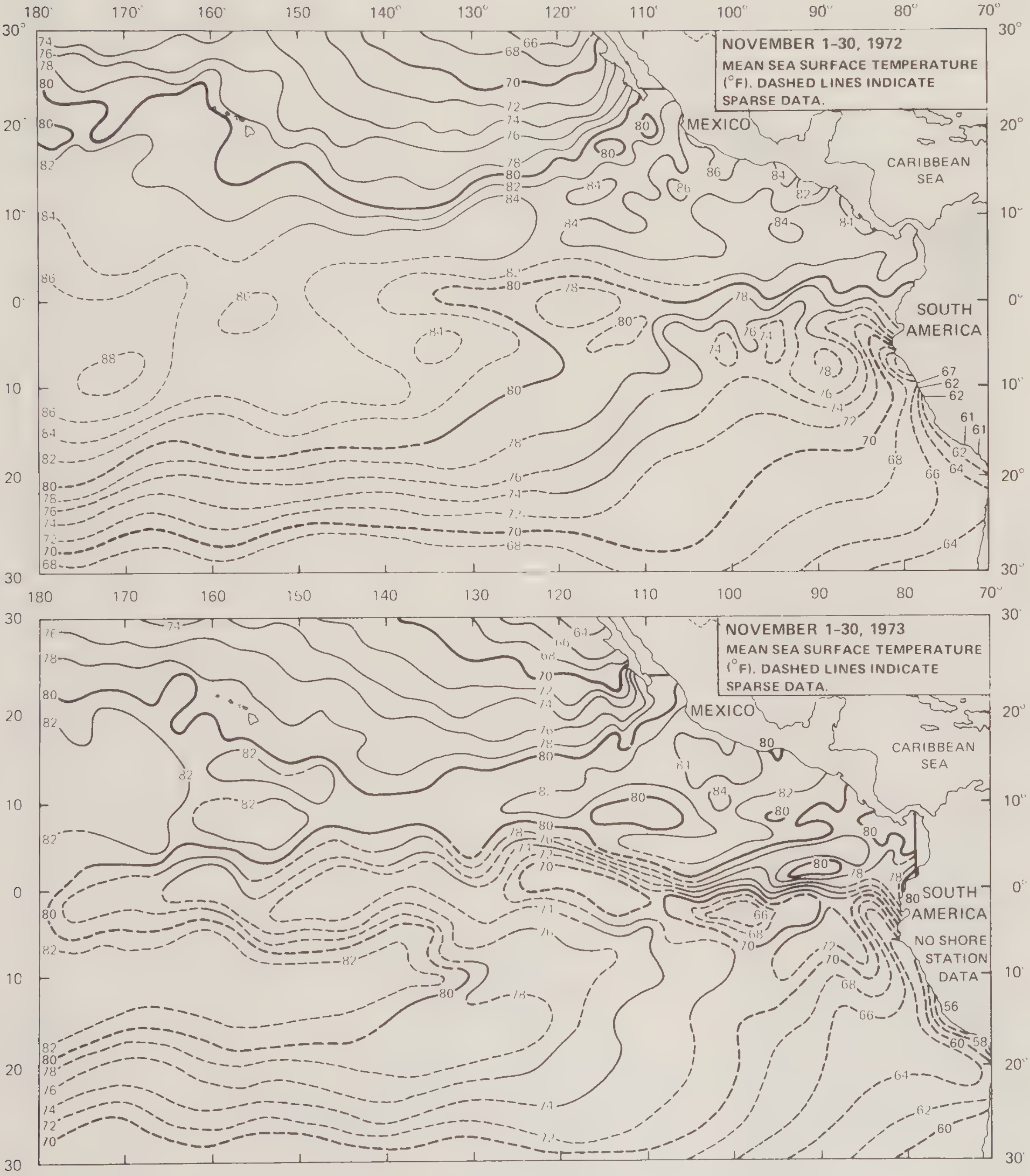
The El Niño off the west coast of South America is a short-term climatic anomaly that has a large effect on the anchoveta fishery. This effect has been widely discussed. Here we would like to point to its tremendous impact on fish meal and soybean meal prices in the United States, which quadrupled shortly after the onset of the 1972 El Niño (fig. 4).

Differences between El Niño and non-El Niño years are reflected in large variations in sea surface temperatures not only along the South American coast in the area of the anchoveta fishery, but over vast areas of the equatorial Pacific. For example, the sea surface temperature in the eastern equatorial Pacific in November 1972, an El Niño year, was up to 5°C (10°F) warmer than in November 1973, a non-El Niño year (fig. 5). These large differences also are reflected in changes in the atmospheric circulation.

Bjerknes (1969) described anomalous conditions in the equatorial Pacific during El Niño years. He related high heat supply in the equatorial Pacific during these years with intensification of the Hadley circulation, increased flux of angular momentum, and intensified mid-latitude westerly and trade winds. He indicated that these teleconnections affect the weather over the North American continent and believed that regular monitoring of the sea surface temperature in the tropical Pacific is indispensable in long-range forecasting for North America. Namias (1972 and other studies) also stressed the importance of the oceans in long-range weather prediction.

Quinn (1972) examined air-sea interactions in the equatorial Pacific and the associated trough and ridge development over the North Pacific and the continental United States. The type of atmospheric circulation that prevails over the eastern part of the United States appears to affect the eastern seaboard shrimp fishery. Williams (1969) has shown that a good fishery tends to follow warm winters along the eastern seaboard and a poor fishery tends to follow cold winters. Johnson and McLain (1975), examining the type of circulation related to warm and cold years, have used marine surface observations to describe the anomalously warm February of 1949 and the anomalously cold February of 1958 along the eastern seaboard (fig. 6). They also identified the types of atmospheric circulation that tend to typify these extreme conditions (fig. 7).

During warm winters, as in 1949, ridge development at the 700 mb level tends to block storms of northern origin. Consequently, air masses of tropical character predominate and water temperatures are warmer. During cold winters, as in 1958, trough development over the eastern United States at the 700-mb level tends to bring cold continental air masses over the southeastern seaboard. Consequently, increased heat loss through evaporation and conduction of sensible heat results in colder water temperature. Thus it


180° 170° 160° 150 140° 130° 120° 110° 100° 90° 80° 70°
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NOVEMBER 1-30, 1972
MEAN SEA SURFACE TEMPERATURE (°F). DASHED LINES INDICATE SPARSE DATA.
MEXICO
CARIBBEAN SEA
SOUTH AMERICA
66 68 70 72 74 76 78 80 82 84 86 88
67 62 61 64
NOVEMBER 1-30, 1973
MEAN SEA SURFACE TEMPERATURE (°F). DASHED LINES INDICATE SPARSE DATA.
MEXICO
CARIBBEAN SEA
SOUTH AMERICA
NO SHORE STATION DATA
56 58 60 62 64 66 68 70 72 74 76 78 80 82 84

Fig. 5. Mean sea-surface temperatures, eastern tropical Pacific, November 1972 and 1973. (U.S. National Marine Fisheries Service, 1972, 1973.)

appears that ridge development in the upper air circulation is more favorable to the shrimp fishery than is development of a trough.

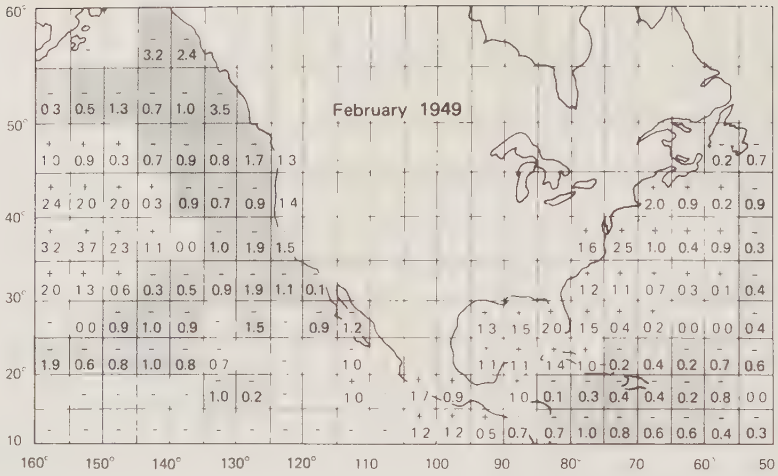
Conclusion

The rising demand for fishery products makes fishery management an increasingly important function. In the past, environmental considerations were not a part of management models. Our illustrations show that this omission can lead to management errors. For example, had the relationship between the Pacific mackerel and the environment been known earlier, correct management procedures could have prevented collapse of the fishery.

An important part of fishery management is prediction of year-class strength. A large year-class, for example, may lead to a large increase in fishing effort, which continues after the year-class has been harvested, leading to overcapitalization and over fishing in subsequent years of reduced stock size. A large year-class, followed by several poor year classes, is potentially disastrous to fish stocks and to the fishing industry. The prediction of environmental changes and their effect on year-class strength, therefore, is a major goal of our research.

In our examples we have tried to point out that relating changes in fisheries with variations in environmental conditions depends upon the availability of long-term marine environmental data series. The only source for such series are the historical files of marine meteorological observations.

Once a fishery-environment relation has been established, current marine meteorological observations become the basis for predictions of fish abundance. Clearly, the World Meteorological Organization's foresight in sponsoring the archival of a vast amount of marine meteorological data and in continuing a strong



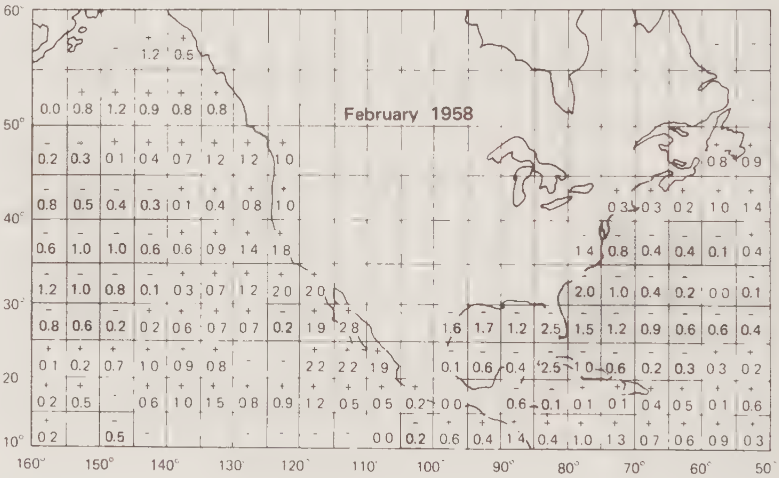
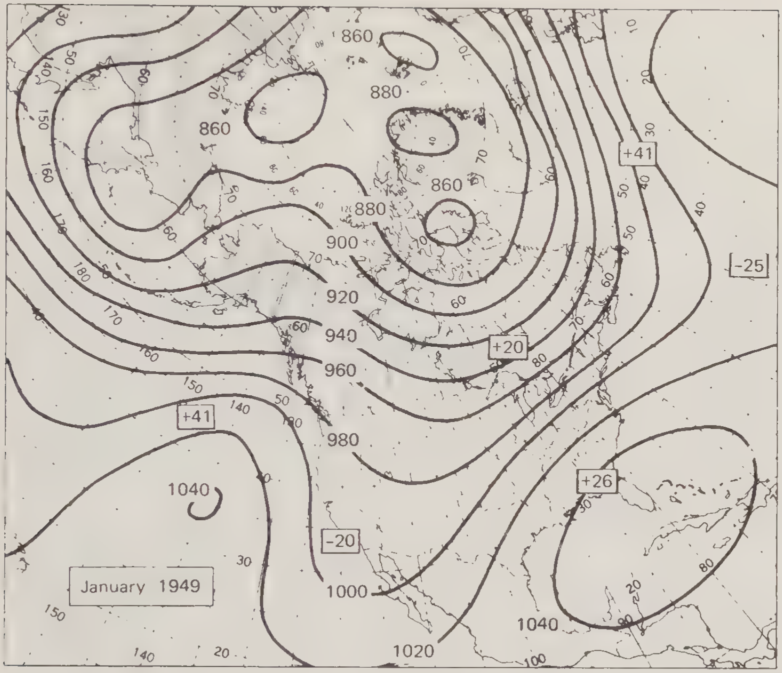
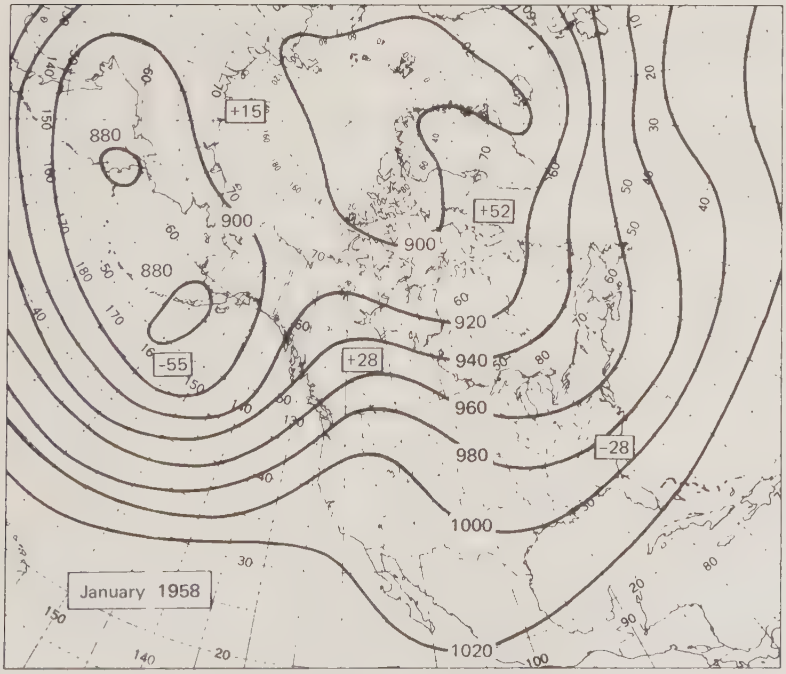


Fig. 6. (Above.) Sea-surface temperature anomalies (°C). Shaded areas are colder than the 20-yr (1948-67) mean. (Johnson and McLain, 1975.)

Fig. 7. (Opposite page.) 700-mb heights and departures from normal (in boxes) in tens of feet. (Johnson and McLain, 1975.)





marine program will have a significant impact on our ability to manage fishery resources and to help feed the hungry of the world.

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* Presented at the World Meteorological Organization's Technical Conference on the Applications of Marine Meteorology to the High Seas and Coastal Zone Development, 22-26 Nov. 1976, Geneva, Switzerland.

Env. Biol. Fish., Vol. 2, No. 2, pp. 185–188, 1977

Estimation of caloric content for fish biomass

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Keywords:
Calories, Fish biomass, Energy content, Skipjack tuna, *Katsuwonus pelamis*, Starvation

Synopsis

Analyses of tissues from just-caught and captive, starved skipjack tuna, *Katsuwonus pelamis*, indicated a significant effect of starvation on water, ash, and caloric content. Caloric content of just-caught whole fish was 1.45 to 1.48 kcal g^{-1} wet weight and was directly comparable to values determined for white muscle (edible) tissue samples. Examination of recent literature yielded caloric data for 81 fish species. These data plus those from our study indicated that the assumption 1 g wet weight = 1 kcal can result in substantial error. Less than 40% of the data were within the range 0.90–1.10 kcal g^{-1} wet weight. A linear relationship between caloric content (Y) and percent water (X) derived as $Y = 5.537 - 0.059X$ resulted in an overall improvement in estimation of caloric content.

Introduction

Studies of fish energetics frequently require an estimate of caloric value to convert biomass to its energy equivalent. The current convention is that 1 g of wet biomass is roughly equivalent to 1 kcal (Winberg 1960, Winberg & Edmondson 1970, Warren 1971) and is widely used in reports ranging from single species modeling studies (Norstrom, McKinnon & deFreitas 1976) to large-scale applications on a global basis (Crisp 1975, Rounsefell 1975). A report by Brett (1973) and a compilation of data by Sidwell et al. (1974) indicate that a single conversion does not suffice for universal application to fishes when accuracy greater than ± 30% is desired. Summarizing data for many consumer species, Pandian (1975) concluded that intraspecific variation of up to 1.5 kcal g^{-1} dry weight may be due to nutritional history.

We propose a linear relationship between energy content and percent water of wet weight to estimate more accurately the caloric equivalent of fish biomass. Caloric content of whole fish, red muscle, and white muscle of skipjack tuna, *Katsuwonus pelamis*, was determined from starved captive fish and from fish just caught at sea to test this hypothesis and to estimate the energy content of scombrid fishes.

Method and materials

Skipjack tuna were from pole-and-line catches near Hawaii. Four fish captured on 29 March 1974 were immediately killed, weighed, and measured. Two of the four were frozen intact. The remaining two were dissected and samples of red and white muscles were removed, weighed, and frozen for later analyses.

Fish captured on 2 April 1974 were maintained alive for 10 days without food in a tank at the Kewalo Research Facility (Nakamura 1972) of the National Marine Fisheries Service. Four fish were then removed, killed, weighed, and measured; two were frozen intact and two were dissected for muscle samples as above. Initial weights prior to starvation were not obtained because skipjack tuna do not survive handling.

Whole fish and muscle samples were oven dried at 70° C up to 17 days, then at 85° C to a constant dry weight. Entire samples were ground and homogenized, redried, then stored in a dessicator. Approximately 1 g subsamples were removed for measurement of ash and caloric content. The ash fractions, three replicates per sample, were determined by burning subsamples overnight in a muffle furnace (640°–650° C). Calorimetry, five replicates per sample, was performed with a Parr* oxygen bomb calorimeter as generally prescribed in American Society for Testing Materials (1966), except that acid titrations were not performed because our previous experience had indicated that the corrections are insignificant for within-taxon comparisons.

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Received 22.6.1976 Accepted 10.2.1977

* Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Results

Caloric yields of the two just-caught skipjack tuna (Table 1) were very similar: 1.45 and 1.48 kcal g^{-1} wet weight. White muscle samples (Table 1) generally approximated whole fish energy yield in wet weight units among both just-caught and starved fish. Thus edible portions, for which most calorimetry data are available, can provide a reasonable estimate for the total animal. Red muscle is a small proportion of total muscle and, while it appears to have a higher energy content, inclusion with white muscle would not greatly influence an estimate of whole fish energy content from the edible portion.

Starvation had a significant effect on caloric, water, and ash content (Table 1). Extensive comparisons among tissues and treatments are precluded owing to our small sample sizes. Even so, a two-way analysis of variance performed with data on calories per gram dry weight did indicate a significant ($P < 0.05$) effect of starvation on caloric content.

Several trends are clear and consistent with those reported elsewhere (Brett 1973). Both water and ash fractions were greater for starved fish while energy content per unit weight decreased with starvation. Caloric differences were most apparent on a wet weight basis and in red muscle (Table 1). These observations suggest that there is greater utilization of high energy sources (e.g. fat or oil) from red muscle than white muscle during starvation. More important to the problem of estimating energy content of whole fish, energy content on a wet weight basis is inversely related to body water content. Changes in energy and water content may be due to different conditions of reproductive activity, depletion of energy reserves during migration, and/or seasonal variation in lipid content due to changes in food quality and consumption rates (Pandian 1975).

Discussion

The caloric content of skipjack tuna is considerably higher than the 1.0 kcal g^{-1} rule of thumb used in fish bioenergetic studies. Caloric density is altered by starvation. Fasted, exercised sockeye salmon, *Oncorhynchus nerka*, also demonstrated significant increases in body water content and decreases in energy content per unit wet and dry weight (Brett 1973). In addition, of the 79 species represented in data tabulated by Sidwell et al. (1974) only 32 had caloric values

Table 1. Caloric values of whole fish, red muscle, and white muscle of just-caught and starved (10 days) skipjack tuna, *Katsuwonus pelamis.* Means for percent ash of wet weight and kilocalories per gram dry weight are given for each fish plus or minus one standard error.

Tissue (treatment)	Fish wet weight (kg)	Fork length (cm)	Percent of wet tissue weight		Kilocalories per gram weight		
			Water	Ash	Wet	Dry	Ash-free dry
Whole fish (just caught)							
Fish #1	1.48	43	71	3.38 ± 0.05	1.45	4.97 ± 0.02	5.62
Fish #4	1.56	44	71	3.19 ± 0.02	1.48	5.04 ± 0.01	5.65
Whole fish (starved)							
Fish #5	1.56	45	74	3.22 ± 0.02	1.22	4.75 ± 0.01	5.43
Fish #7	2.28	50	75	3.56 ± 0.03	1.13	4.54 ± 0.02	5.29
Red muscle (just caught)							
Fish #2	1.50	43	71	1.20 ± 0.04	1.63	5.58 ± 0.02	5.82
Fish #3	1.42	43	72	1.05 ± 0.02	1.52	5.42 ± 0.02	5.63
Red muscle (starved)							
Fish #6	1.48	44	76	1.00 ± 0.01	1.30	5.40 ± 0.01	5.64
Fish #8	2.57	52	74	1.08 ± 0.01	1.38	5.41 ± 0.01	5.65
White muscle (just caught)							
Fish #2	1.50	43	72	1.25 ± 0.04	1.46	5.20 ± 0.01	5.44
Fish #3	1.42	43	72	1.19 ± 0.01	1.43	5.17 ± 0.02	5.40
White muscle (starved)							
Fish #6	1.48	44	76	1.16 ± 0.03	1.28	5.21 ± 0.01	5.47
Fish #8	2.57	52	76	1.22 ± 0.07	1.21	5.08 ± 0.01	5.35

between 0.90 and 1.10 kcal g^{-1} wet weight.

The results of starvation treatments (Table 1 and Brett 1973) and inspection of data summarized by Sidwell et al (1974) confirm a strong interaction between tissue water content and energy yield per unit weight. That relationship would be expected, of course, in that the energy values are associated with the dry weight (i.e., organic plus ash) fraction. Analysis of skipjack tuna tissues emphasizes the potential error associated with accepting the energy value of 1 kcal g^{-1} wet weight as well as that associated with the assumption that weight loss is directly equivalent to energy expenditure. Weight loss underestimates energy loss during starvation because hydration occurs as the hydrophobic lipid reserves are utilized. Caloric density decreases but weight changes are not strictly proportional due to simultaneous increase in tissue water content. The reverse is very probably true as fish are increasing lipid reserves; energy stored would be underestimated by weight increments alone.

Caloric values of other tuna species also tend to be high, ranging from 0.98 kcal g^{-1} wet weight for bigeye tuna, *Thunnus obesus*, to 1.69 kcal g^{-1} for Atlantic mackerel, *Scomber scombrus* (Sidwell et al. 1974). In general, caloric values are highest for those fishes that are highly active (e.g. Scombridae) or those that migrate substantial distances (e.g. Salmonidae and Scombridae).

Recognizing that results from calorimetry and/or proximate analysis are desirable but not often available to investigators of fish energetics, we propose that an easily measured parameter – per cent water of live weight – will provide the basis for a more accurate estimate of energy content. The relationship between caloric value and water content of fish biomass is estimated by the regression equation given in Figure 1.

When all data in Figure 1 are considered, less than 40% of caloric measurements are within ± 10% of the estimate from the convention of 1 g wet weight = 1 kcal. An overall improvement comes from use of the regression where approximately 60% of caloric measurements are within 10% of the estimate. The coefficient of determination (r^2) is 0.66 for the regression. For skipjack tuna, application of the 1 g wet weight = 1 kcal assumption results in estimates that are low by about 30%. Application of the regression equation (Fig. 1) results in estimates that are low by about 10%. Use of the regression constitutes a significant improvement for fish with a high energy yield and low water content like a tuna but little or no improvement for fish with water contents between 75% and 80%.

Thus an improved estimate of energy content for fish may frequently be made with this regression equation (Fig. 1) or one similarly derived when direct

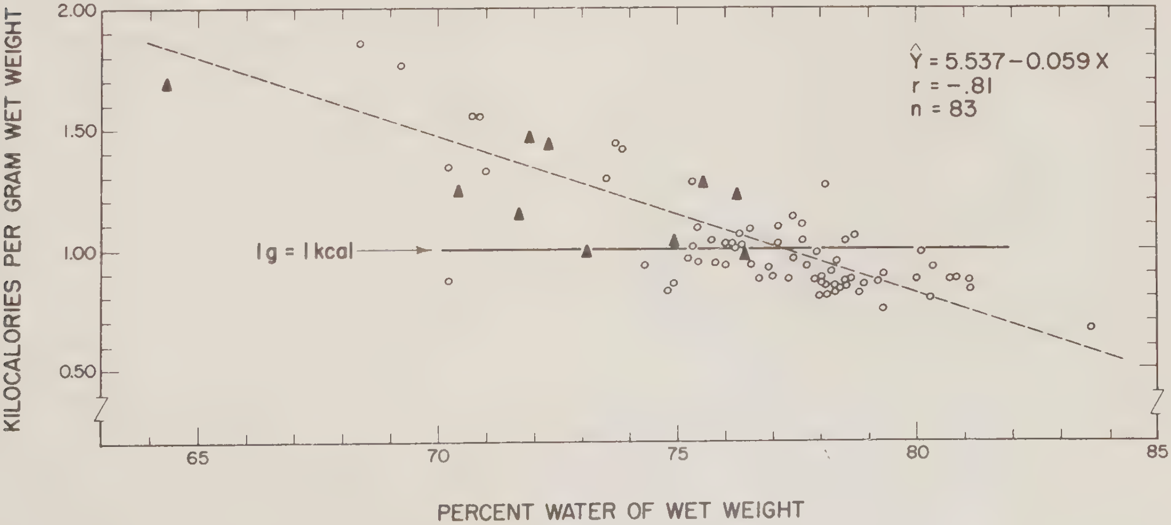

Fig. 1. Relation between water content and energy yield of fish biomass. Data for the 81 species represented are from Brett (1973), Sidwell et al. (1974), and our study (Table 1). Included are two data for starved sockeye salmon and skipjack tuna. Triangle data are those for species of the family Scombridae.

measurements of caloric content are not available. Data summarized here suggest that the relationship can be applied both within and between taxa of fishes. Within a taxon, more accurate data on temporal variation in energy content, particularly that associated with lipid reserves, may be determined from regression analysis of some caloric data in combination with regular monitoring of the more readily measured body water content. Ontogenetic changes may be similarly determined (Pandian 1975) but should include a correction for increased inorganic (ash) fractions of the dry weight due to increased proportions of total weight associated with structural tissues.

Acknowledgments

This study was supported in part by Contract Nos. 03-3-208-37, 03-4-208-274, and 03-5-208-184 from the U.S. Department of Commerce, NOAA, National Marine Fisheries Service and by a grant from the University of Wisconsin Brittingham Oceanography Fund. We thank John Gryskiewicz for technical assistance in calorimetric analyses.

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THE UPTAKE, DISTRIBUTION, AND DEPURATION OF ^{14}C BENZENE AND ^{14}C TOLUENE IN PACIFIC HERRING, *CLUPEA HARENGUS PALLASI*

This note is a sequel to Korn et al. (1976), where uptake, distribution, and depuration of ^{14}C benzene were examined in striped bass, *Morone saxatilis,* and northern anchovy, *Engraulis mordax*. Like benzene, toluene is a prevalent, water-soluble, and toxic monoaromatic component of petroleum and associated products. According to Anderson et al. (1974a), toluene is second only to benzene as the most abundant aromatic oil component in the water-soluble extracts of southern Louisiana and Kuwait crude oils (6.75–3.36 μl/liter benzine; 4.13–3.62 μl/liter toluene, respectively).

Although levels of the volatile aromatics are thought to be low in areas subject to chronic oil exposure, few actual measurements have been made. Further, if fish can accumulate benzene and if energy is required to metabolize, detoxify, and depurate these aromatics, long-term physiological and population effects are possible.

In this study, a comparison of the uptake, distribution, and depuration of ^{14}C benzene and ^{14}C toluene, at a low sublethal concentration [100 parts per billion (ppb)], was undertaken to determine which of these prevalent aromatics may pose the greatest problem. It was hypothesized that, although toluene is less soluble in seawater (Anderson et al. 1974a), it may be more toxic and exhibit greater accumulation levels and persistence. Our previous work with striped bass and northern anchovy indicated other tissues that should be examined, such as kidney, pyloric caeca, gonad, and intestine, and in the present comparison, residues in the additional tissues were measured. Pacific herring, *Clupea harengus pallasi*, were selected as test animals because of their importance as estuarine and nearshore forage fish for many important recreational and commercial species, including striped bass and chinook salmon.

Methods

Pacific herring were obtained from a San Francisco Bay bait dealer and were transported directly to the Tiburon Laboratory dock. The fish were acclimated under test conditions for at least 2 wk in 2,000-liter tanks. Fish were not in spawning condition.

In each of two separate studies, 10 fish were placed into each of six 660-liter fiber glass tanks and further acclimated for 1 wk before exposure. Salinity and temperature were 24‰ and 9°–11°C, respectively, during the acclimation and test periods. In the first study, fish were exposed to 100 nl/liter (ppb) ^{14}C benzene (4.2 dpm/ng specific activity). In the second study, fish were exposed to 100 nl/liter (ppb) ^{14}C toluene (3.2 dpm/ng specific activity). In both studies, one of the six tanks was a control, with no exposure. Exposures were static (single dose with delining concentration) for 48 h, preceded and followed by a continuous water flow of 2 liters/min.

Water samples for radiometric aromatic analyses were taken from all tanks at 0, 6, 24, and 48 h after initial dosage. Gallbladder, intestine, pyloric caeca, gill, brain, liver, muscle, kidney, and immature male and female gonad tissues were sampled for radiometric analyses at 6 h, then daily for 7 days.

Methods of exposure and radiometric analyses are identical to Korn et al. (1976), except that the tissues from fish exposed to toluene were digested at 50°C for 24 h.

Since accumulation levels in the gallbladder were based solely on radiometric analysis of the ^{14}C present and could include metabolites of the monoaromatics as well as unchanged benzene or toluene, an additional study was made to interpret the residue. Two groups of fish, with six fish per tank, were exposed to 100 nl/liter ^{14}C benzene (1 tank), and 100 nl/liter ^{14}C toluene (1 tank) for 48 h. Exposure was the same as in the above experiments. At the end of the 2-day exposure, the gall bladders were removed, weighed, and extracted with 0.2 ml trifluorotrichloroethane-Freon.[1] The extracts were analyzed for benzene and toluene by gas chromatography (Benville and Korn 1974). Efficiency of extraction was not determined and therefore the gas chromatography analyses were more qualitative than quantitative.

Results and Discussion

There were no mortalities in either exposed or control fish. Unlike herring exposed during spawning condition (Struhsaker 1977), no abnormal behavior was noted, thus immature herring appear less sensitive to exposures than mature herring in spawning condition.

The concentration of benzene and toluene in seawater in all tanks declined linearly ($\hat{Y} = a + bX$ where $\hat{Y}$ = concentration in microliters per liter, a = initial concentration in microliters per liter, b = rate of decline in microliter per liter per hour, and X = time in hours), during the 48-h static exposure, as follows:

Item	*Benzene*	*Toluene*
Total no. samples	20	20
a ($\hat{Y}$-intercept)	0.094997	0.09195
b	−0.0006075	−0.0007587
Percentage of initial concentration remaining:		
24 h	85	80
48 h	69	60

The equation for decline in benzene and toluene is probably a function of the volume of seawater. In earlier studies, at smaller volumes, decline was exponential over the 48-h static exposure. At the volume in these experiments it was linear, but probably would have been exponential over a longer time period. The rate of decline appears to decrease with increasing volume.

In all herring tissues, toluene accumulated to higher levels than did benzene (Table 1), despite the faster loss of toluene compared with benzene from the test solution. Certain trends were common to both aromatic components. The tissue exhibiting the highest accumulation was the gallbladder (3.1 nl/g benzene, 34 nl/g toluene, maximum level). The lowest level of maximum accumulation was found in the immature gonad (0.24 nl/g benzene, 0.44 nl/g toluene). Pyloric caeca and intestine contained varying amounts of bile and therefore had a wide range of ^{14}C activity and a resulting wide variance in calculated concentrations.

Benzene was accumulated up to 31 times the initial water concentration (gallbladder) and toluene reached 340 times the initial water concentration (gallbladder).

In most tissues, and for most components, maximum accumulation levels were reached rapidly. Within 24 h, maximum residues were obtained in all tissues except the gallbladder and pyloric caeca. Toluene accumulated to the maximum level (0.25 days) before benzene peaked (1–2 days) in all tissues except the gallbladder and intestine.

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[1] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Residues of benzene and toluene and/or metabolites (mean nl/g±SE) accumulated during and after a 48-h exposure to 100 nl/liter (ppb) ^{14}C benzene or 100 nl/liter (ppb) ^{14}C toluene in the tissues of *Clupea harengus pallasi*. Number of samples in parentheses.

Tissue and compound	Time (days) from start of exposure[1]							
	Uptake			Depuration				
	0.25 (6 h)	1	2	3	4	5	6	7
Gallbladder:								
Benzene	0.37±0.075 (4)	2.1±0.71 (5)	3.1±0.48 (5)	2.7±1.5 (3)	0.56±0.30 (3)	0.92±0.79 (4)	0.60±0.14 (4)	0.61 (1)
Toluene	4.6±3.4 (5)	30±11 (5)	27±15 (5)	34±17 (5)	19±9.0 (5)	1.7±0.95 (5)	0.24±0.49 (3)	6.0±4.9 (2)
Intestine:								
Benzene	0.83±0.78 (4)	0.42±0.28 (5)	0.61±0.55 (5)	0.16 (1)	—[2] —	0.087 (1)	0.081 (1)	— —
Toluene	3.9±2.4 (5)	2.3±2.1 (4)	2.1±1.7 (5)	0.70±0.7 (5)	0.09±0.014 (2)	0.092±0.013 (3)	0.11±0.025 (2)	0.13±0.70 (3)
Pyloric caeca:								
Benzene	0.058±0.34 (5)	0.63±0.38 (5)	0.64±0.38 (5)	0.095±0.039 (3)	— —	0.056 (1)	— —	— —
Toluene	3.6±3.6 (5)	1.8±0.32 (5)	2.4±1.4 (5)	0.77±0.46 (5)	0.23±0.94 (5)	0.13±0.03 (5)	0.11±0.037 (5)	0.16±0.081 (4)
Gill:								
Benzene	0.51±0.12 (5)	0.61±0.33 (5)	0.73±0.46 (5)	0.073 (2)	0.068 (1)	— —	— —	— —
Toluene	1.8±0.58 (5)	1.2±1.2 (5)	1.0±0.96 (5)	0.20±0.12 (5)	— —	— —	— —	— —
Brain:								
Benzene	0.74±0.11 (5)	0.75±0.14 (5)	0.62±0.052 (5)	0.59 (2)	— —	— —	— —	— —
Toluene	2.1±0.19 (5)	2.0±0.28 (5)	1.5±0.18 (5)	0.13±0.073 (3)	— —	— —	— —	— —
Liver:								
Benzene	0.45±0.070 (5)	0.53±0.096 (5)	0.50±0.067 (4)	— —	— —	— —	— —	— —
Toluene	1.5±0.44 (5)	1.4±0.44 (5)	1.2±0.13 (5)	0.36±0.15 (5)	0.23±0.05 (4)	— —	— —	— —
Muscle:								
Benzene	0.41±0.22 (5)	0.63±0.36 (5)	0.44±0.33 (4)	0.035 (1)	0.066 (1)	— —	— —	— —
Toluene	1.3±0.80 (5)	0.52±0.28 (5)	0.66±0.71 (5)	0.33 (2)	— —	— —	— —	— —
Kidney:								
Benzene	0.32±0.066 (5)	0.32±0.066 (5)	0.40±0.12 (5)	— —	— —	— —	— —	— —
Toluene	1.3±0.50 (5)	1.1±0.40 (5)	0.75±0.33 (5)	0.18±0.099 (4)	— —	— —	— —	— —
Gonad:								
Benzene	0.15±0.021 (5)	0.24±0.062 (5)	0.21±0.10 (5)	— —	— —	— —	— —	— —
Toluene	0.43±0.24 (5)	0.44±0.21 (5)	0.44±0.28 (4)	0.16 (1)	— —	— —	— —	— —

[1] Exposure terminated after 2 days; then fish remained in flowing seawater for 5 days.
[2] — = nondetectable levels.

Residues were depurated rapidly, with most tissues having nondetectable amounts after 3–4 days (1–2 days after termination of exposure). The gallbladder, intestine, and pyloric caeca retained residues through the duration of the study (7 days).

In the experiment in which gas chromatographic analyses were performed on the gallbladder, no detectable benzene (<0.1 nl/g) was measured. Gas chromatography analysis resulted in only 0.56–1.5 nl/g toluene. This indicates that most or all of the radioactivity measured by liquid scintillation in the gallbladders of fish exposed to benzene is not the parent compound, but one or more metabolites. Fish exposed to toluene had a small amount of the parent compound as opposed to metabolites (1.5 nl/g toluene maximum, compared with 27 nl/g expected [Table 1]).

The above result and the occurrence of delayed depuration in the gallbladder, intestine, and pyloric caeca supports the contention that benzene and toluene are metabolized in the liver, stored in the gallbladder, then passed into the intestine and are excreted with the feces. This agrees with Roubal et al. (in press) who found high levels of benzene metabolites in the liver and gallbladder of salmon which had previously received intraperitoneal benzene injections. This also agrees with our previous results with benzene in other fishes (Korn et al. 1976), results of Neff (1975), and with work by Lee et al. (1972) who demonstrated metabolism of polycyclic aromatics in the liver and subsequent storage in the gallbladder. Studies with polycyclic aromatics (naphthalene, benzpyrene) by other investigators (Lee et al. 1972; Anderson et al. 1974b; Neff 1975; Roubal et al. in press) indicate higher accumulation levels and slower depuration than we have found with benzene and toluene. However, different species are involved, and these higher aromatics are also less prevalent in the water-soluble extract of crude oil.

The results of this study are generally consistent with our previous work exposing striped bass and northern anchovy to ^{14}C benzene at the same initial concentration and exposure period (100 nl/liter for 48 h; Korn et al 1976), except for the considerably higher accumulation in the anchovy than in the other species. This is probably primarily a result of the higher stress, activity level, and scale and mucus loss in anchovy while in captivity.

The gonads sampled in this study were immature and showed low accumulation levels. In another study exposing mature spawning herring to 100 nl/liter benzene for 48 h (Struhsaker 1977), higher accumulation occurred in the ovary, with associated deleterious effects on the ripe ovarian eggs and on development of larvae subsequent to exposure of the parental females.

Of the two components studied here, toluene would appear to be potentially a greater problem to fish. Toluene could be rapidly accumulated to high levels in fish after even a brief contact during an oil spill. Since toluene is one of the more prevalent water-soluble oil components, further research on the effects and uptake of this component are indicated. Further, chronic exposures are probably of more importance to the survival of fish populations than are spills, and studies of long-term exposure to chronic concentrations should be made.

Finally, the probability that benzene and toluene are rapidly metabolized or converted to metabolites (possibly phenol, which is also highly toxic) leads to the need for metabolite research. Uptake studies with phenolic metabolites would be of interest, as would be the determination of uptake over extended time intervals.

Acknowledgments

We acknowledge the considerable assistance of other members of the Physiology Investigation, Tiburon Laboratory, particularly Pete Benville for the gas chromatography analysis. We also thank Stanley Rice, Northwest and Alaska Fisheries Center, Auke Bay Laboratory, and Jerry M. Neff of Texas A&M University for their critical reviews of the manuscript.

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REPRINT FROM
Calif. Fish and Game, 63(4) : 210-218. 1977

ACCLIMATION AND REARING OF STRIPED BASS LARVAE IN SEA WATER [1]

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For the first time, striped bass larvae were reared under laboratory conditions in sea water (salinity 33.73°/∞) for more than a year. Five-day-old larvae, hatched in fresh water, were rapidly acclimated to 20, 40, and 60% sea water and reared in these salinities for 33 days. The earliest time the larvae could survive transfer to full sea water was at 28 days of age; metamorphosis occurs between 28 and 35 days.

Separate tests were made to determine the effects of different salinities on larval growth and survival. Growth over a period of 4 weeks was measured in 20, 40, and 60% sea water with a control group in fresh water, but no adverse effect on growth was observed on larvae in diluted sea water. In tests of salinity tolerance, 1-day-old eggs and larvae after hatching in fresh water were rapidly acclimated to different salinities and reared without food for 9 and 12 days. Survival was best when the larvae were acclimated just after hatching in 10% sea water. Diluted sea water proved to be better for larval survival than fresh water alone.

INTRODUCTION

A relative lack of predator fishes in the limnetic zone of large warmwater impoundments in California is considered to be a major factor limiting potential game fish production (Anon. 1971). Attempts to correct this deficiency have centered largely on the introduction of limnetically oriented forage and game fish species. Threadfin shad (*Dorosoma petenense*) were introduced from Tennessee in 1953 (Kimsey 1954) and this forage species is now firmly established in many reservoirs throughout California (Burns 1965). Game fish species stocked in selected reservoirs in efforts to more fully utilize shad as forage include crappie (*Pomoxis* sp) (Goodson 1966), white bass (*Morone chrysops*) (von Geldern 1964), and striped bass (*Morone saxatilis*) (Wilson and Christenson 1965). In recent years, a variety of salmonids have also been successfully introduced into warmwater reservoirs containing well-oxygenated hypolimnions (Rawstron 1973, Wigglesworth and Rawstron 1974).

While crappie and white bass may be normally expected to maintain self-sustaining populations, the development of successful striped bass fisheries is largely dependent on maintenance stocking programs. Such programs involve the introduction of fingerlings or yearlings (Bailey 1975), and California has given high priority to an evaluation of striped bass stocking and the possible development of a firm source of fish within our hatchery system.

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[1] Accepted for publication September 1976. This work was performed as part of Dingell-Johnson project California F-18-R, "Experimental Reservoir Management" supported by Federal Aid to Fish Restoration funds.

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An extensive effort has been made across the southern United States to develop the technology for rearing striped bass in freshwater hatcheries (Bailey 1975). Freshwater culture, however, frequently results in heavy mortalities of larval fish. This problem prompted the present study which examines the salinity tolerance characteristics of striped bass larvae as part of a broad program designed to evaluate the feasibility of rearing striped bass in a sea water hatchery.

Increased survival of striped bass eggs and larvae has been reported for periods up to 3 weeks in sea water concentrations ranging from 3% (Albrecht 1964) to 30% (Doroshev 1970, Bayless 1972). Our study is an extension of earlier work and was designed to: (i) determine if striped bass eggs and larvae can be acclimated to higher salinity concentrations, and (ii) determine if larval bass could be reared through metamorphosis in 100% sea water.

METHODS AND RESULTS

Four groups of fertilized striped bass eggs, produced by hormone-induced spawning of ripe fish at the Central Valleys Hatchery of the California Department of Fish and Game, Elk Grove, were shipped by air to La Jolla, California, during May and June 1973. The eggs were hatched in a 122-cm (4-ft) diameter fiberglass trough containing tap water with chlorine reduced to 1.5 ppm. Eggs were kept from settling to the bottom by bubbling air. The incubation period varied from 40 to 48 hours at 18.5 ± 1 C (65 ± 2 F). Between 80 and 95% of the larvae hatched out from the first three groups of eggs received, but only 15 to 20% hatched in the last group due to poor fertilization. For this reason, testing of 1-day-old eggs from the last group was abandoned after hatching. Eggs or larvae for salinity tests were hand counted and transferred into experimental containers. Because of different experimental techniques in each of the three experiments to follow, we have elected to give details of each experiment separately.

Survival of Striped Bass Larvae After Exposure to Different Salinities

Survival after exposure to different salinities was measured using 1-day-old eggs and 1-day-old larvae hatched in fresh water. Larvae 8 to 14 hours after hatching were termed 1-day-old. One-day-old eggs were 16 to 20 hours old as determined from the time fish were artificially spawned at the hatchery. The various stages of development of our eggs and larvae closely resembled those illustrated by Bayless (1972). Twenty-five eggs or larvae were transferred into 4 l (1.06-gal) glass jars, each containing a different volume of tap water, so that after the gradual addition of La Jolla sea water (salinity 33.73‰), the final volume of water was 2½ l (0.66 gal). The acclimation time varied from 2 to 6 hours, depending on the volume of sea water added. In this manner, the desired salinity and stocking density of 10 eggs or larvae per liter was obtained. All the jars were placed inside a water table with running sea water at 19 ± 0.5 C (66 ± 1 F).

In this experiment, we used eggs and larvae from three different groups of eggs received from Elk Grove. Three similar experiments were done in succession. The first was terminated 9 days after acclimation, the second and third after 12 days. One-day-old eggs and 1-day-old larvae in the 9-day experiment were tested separately in 20, 40, 60, 80, and 100% sea water and, in the case of 12-day experiments in 10, 20, 30, 40, 50, 60, and 70% sea water. Eggs in the last 12-day experiment, were not tested due to poor hatch. For each experiment a control group was kept in fresh water, and replicate jars were set up for all salinities tested as well as for the controls.

No food was given to the larvae throughout the experiments. Although 6-day-old larvae commence feeding (our observation agrees with Bayless 1972), nearly all can survive without food for 10 days or longer until complete absorption of their yolk (Mansueti 1958). Dead larvae were removed and counted every day and a terminal count of all survivors was taken at the end.

We saw no abnormal development of the embryos in any salinity tested, although it took 2 to 3 hours longer for the eggs to hatch in 80 and 100% sea water. The larvae appeared shrunken in 80 and 100% sea water and died within 72 and 48 hours, respectively. Less than 50% of the larvae survived in salinities higher than 50% sea water, and survival was 75% or more in salinities ranging between 10 and 50% sea water. If more than one test was made, the combined mean for all tests is shown followed by the individual test means in parenthesis (Table 1). These results show that larvae have a high tolerance for sea water up to 50%, if they are acclimated after hatching rather than while in the egg. There was only 27% survival of acclimated larvae after 9 days in 70% sea water, but in the next lower acclimation salinities (i.e. 60% and 50% sea water), there was a remarkable increase in survival. There was a sharp decline in larval survival at the higher salinities after 12 days. We believe this was due to starvation and the stress of higher salinities.

TABLE 1. Percentage Survival of Striped Bass Larvae from 1-Day-Old Eggs and 1-Day-Old Larvae Reared Without Food at 19 C ± 0.5 C [1]

	Percent survival from 1-day-old eggs			*Percent survival from 1-day-old larvae*		
Percent sea water[1]	*After 6 days*	*After 9 days*	*After 12 days*	*After 6 days*	*After 9 days*	*After 2 days*
Fresh water	38(40,36)[2]	30(30,30)	28	64(48,68,76)	52(35,56,64)	49(44,54)
10	82	82	78	95(90,100)	94(90,98)	93(90,96)
20	78(92,64)	72(84,60)	58	93(98,92,90)	92(98,88,90)	82(82,82)
30	82	68	66	94((98,90)	91(98,84)	78(84,72)
40	77(88,66)	71(84,58)	50	87(88,84,88)	85(88,84,84)	74(80,68)
50	76	54	44	84(84,84)	73(70,76)	53(56,50)
60	34(22,46)	9(8,10)	2	63(84,78,26)	47(54,70,16)	27(50,4)
70	—	—	—	28(58,0)	27(54,0)	—
80	0	0	—	0	0	—
100	0	0	—	—	—	—

[1] Salinity of 100% seawater was $33.73^{\circ}/_{oo}$.

[2] In instances where more than one test was conducted, the combined mean of all tests is shown, followed by the individual test means in parenthesis.

Sea water with reduced salinity is beneficial for the well being of the eggs as evidenced by the enhanced survival of eggs in 10% sea water compared to those in fresh water.

TABLE 2. Increase in Dry Weight (mg) of Striped Bass Larvae Fed Brine Shrimp, Nauplii *Artemia* sp. at 18 C ± 0.5 C, N = 500 for Each Salinity

		Salinity of 100% sea water = 33.73 ‰							
		Fresh water		*20% sea water*		*40% sea water*		*60% sea water*	
Age (days)	*Sample Size (number of larvae)*	*Range (mg)*	*Mean (mg)*	*Range (mg)*	*Mean (mg)*	*Range (mg)*	*Mean (mg)*	*Range (mg)*	*Mean (mg)*
12	5	0.107–0.185	0.148	0.112–0.277	0.198	0.117–0.227	0.169	0.146–0.223	0.174
19	10	0.093–0.229	0.159	0.123–0.466	0.346	0.114–0.406	0.293	0.155–0.537	0.327
26	10	0.207–0.792	0.480	0.315–0.956	0.738	0.228–0.997	0.645	0.535–1.291	0.892
33	10	0.367–1.384	1.064	0.647–2.598	1.202	0.549–1.363	0.853	0.608–1.931	1.464

TABLE 3. Increase in Total Length (mm) of Striped Bass Larvae Fed Brine Shrimp, Nauplii *Artemia* sp., at 18 C ± 0.5 C, N = 500 for Each Salinity

		Salinity of 100% sea water = 33.73 ‰							
		Fresh water		*20% sea water*		*40% sea water*		*60% sea water*	
Age (days)	*Sample size (number of larvae)*	*Range (mm)*	*Mean (mm)*	*Range (mm)*	*Mean (mm)*	*Range (mm)*	*Mean (mm)*	*Range (mm)*	*Mean (mm)*
5	10	5.3–5.6	5.5	5.3–5.6	5.5	5.3–5.6	5.5	5.3–5.6	5.5
12	5	5.4–6.2	5.9	5.2–6.8	6.0	5.1–6.4	5.8	5.2–6.2	5.7
19	10	5.6–6.8	6.1	5.5–7.6	6.8	5.5–7.3	6.7	5.5–7.6	6.8
26	10	6.2–8.6	7.6	7.5–9.2	8.5	6.3–8.6	7.9	7.5–9.1	8.3
33	10	7.4–9.7	8.9	7.7–11.0	9.0	7.7–9.5	8.4	7.7–9.8	9.3

Effect of Different Salinities on Larval Growth

Five hundred 5-day-old larvae were transferred into each of four 45 l (12-gal) aquaria containing dechlorinated tap water. Sea water was added gradually into three aquaria to produce 20, 40, and 60% sea water; the fourth had fresh water only. Each aquarium was aerated gently, but there was no flow of water. Dead larvae were removed occasionally, and about a quarter of the volume of water in each aquarium was siphoned out once a week from near the bottom and replaced with an equal amount of water of the required salinity. The aquaria had no gravel or substratum on the glass bottom. Temperature was maintained at 18 ± 0.5 C (64 ± 1 F). The larvae were fed brine shrimp, nauplii *Artemia* sp., daily from day 5 until the experiment ended at 33 days.

The total length of ten 5-day-old larvae was measured at the start of the experiment. Thereafter, both total length and dry weight were recorded from a random sample of 10 larvae taken from each aquarium at 7-day intervals, when the larvae were 12, 19, 26, and 33 days old. Total larval length was measured and the larvae were dried in an oven at 60 C (140 F) for a week. The weight of each larva was recorded to within ± 0.2 μg (.00007 oz) on a Cahn balance (Tables 2 and 3).

From age 12 days, i.e., after 1 week of feeding, until age 33 days, growth, as measured by increase in total length, was not different in diluted sea water and in fresh water (Table 3). On the other hand, rate of growth by weight in 60% sea water averaged 0.06 mg/day (.0002 oz), which is more than 25% faster than that in the lower salinities (Table 4). We observed maximal survival in 40% sea water (Table 4). The lowest growth rate in that salinity may have been due to competition for food among the many survivors. On the other hand, the brine shrimp, *Artemia* sp, did not survive well in fresh water and this may have accounted for the slower growth and poor survival.

TABLE 4. Percentage Survival After 33 Days, and Growth Rate for the Last 21 Days of Larvae Reared in Different Salinities Fed Brine Shrimp, Nauplii *Artemia* sp. at 18 C ± 0.5 C.

Percent sea water[1]	*Percent survival*[2] *(N = 500)*	*Growth rate (N = 10)*	
		Dry weight (mg/day)	*Total length (mm/day)*
Fresh water	9	0.044	0.145
20	25	0.048	0.144
40	47	0.034	0.124
60	22	0.060	0.168

[1] Salinity of 100% sea water was 33.73‰.

[2] Does not include 7% larvae killed for length-weight measurements.

Rapid Acclimation of Striped Bass Larvae and Fry to Sea Water

Our goal was to acclimate striped bass larvae to full sea water at the earliest possible age, but, as found earlier, 1-day-old larvae had died within the first 6 days in 80 and 100% sea water. We therefore sought to reduce the mortality of larvae by rearing them initially in 60% sea water and eventually transferring them to higher salinities, until larvae could withstand full sea water. Our criterion for successful acclimation was at least 50% survival of larvae after the increase in salinity.

Larvae reared in a 45 l (12-gal) aquarium containing fresh water were acclimated to 60% sea water within 24 hours at age 5 days. At age 44 days, fry were acclimated again to 95% sea water within 24 hours. At 114 days, these fry were transferred to a 1,900-liter (500-gal) aquarium provided with 100% sea water at 19 ± 2 C (66 ± 3 F).

Larvae up to the age of 37 days were fed a mixed diet of live brine shrimp, nauplii *Artemia* sp and live marine copepods, *Tisbe* sp After that period, fry were fed at least three times a day on trout chow, Oregon Moist Pellets (OMP), chopped anchovies, and squid.

A second batch of larvae reared in a 135 l (35-gal) aquarium containing fresh water was also acclimated to 60% sea water at age 7 days. At age 19 days, five larvae were acclimated to 95% sea water in a 2 l (0.53-gallon) beaker, but none survived beyond 2 days. At age 28 days, another five larvae were acclimated to 95% sea water in 24 hours with 100% survival after 5 days. The remaining untested 34-day-old fry were also acclimated to 95% sea water in 24 hours. We then combined these 31 surviving 96-day-old fry with 16, 115-day-old fry from the previous batch in a 1,900-l (500-gal) aquarium.

The above 47 fry were reared in sea water for 11 months without mortality. Of these, 23 were killed and measured at this time. Only 4 fingerlings were reared for an additional 4 months, when they were measured (Table 5).

TABLE 5. Growth of Striped Bass Fingerlings in Sea Water After Rapid Acclimation as Fry from 60 to 100% Sea Water[1] at 19 ± 2 C.

Age (months)	*Number of fingerlings*	*Range*	*Mean*	*Median*
Total length (cm)				
11	23	10.0–15.0	13.0	13.0
15	4	16.4–23.8	19.3	18.5
Wet weight (g)				
11	23	15.0–47.1	30.7	31.0
15	4	44.0–135.3	77.7	65.7

[1] Salinity of 100% sea water was $33.73\,^{0}/_{00}$.

DISCUSSION

Albrecht (1964) pointed out that striped bass eggs can withstand a moderate increase in salinity and that survival of resulting larvae is best in 3% sea water (chlorides 948 ppm). In his experiments, larvae did not survive beyond 3 days in 40% sea water (chlorides 14,100 ppm), whereas in ours, survival was excellent up to 9 days. Turner and Farley (1971) found that survival of striped bass eggs hardened in fresh water at 14.5, 18.5, and 22 C (58, 65, and 72 F) was higher in 3% sea water (TDS 1,000 ppm) than in fresh water (TDS 163 ppm). They also found that at salinities of 6, 15, and 30% sea water (TDS 2,000; 5,000; and 10,000 ppm) at 14.5 C (58 F) survival was about *twice* as high as at 18 and 22 C (65 and 72 F), and that survival of eggs incubated at salinities from 3 to 30% sea water was about the same. Our results showed a similar trend. Survival of 1-day-old eggs hatched in salinities ranging between 10 and 50% sea water was higher than in fresh water control. On the other hand, larval survival progressively declined for eggs hatched in salinities greater than 10% sea water. Therefore, we do not suggest incubating striped bass eggs at salinities exceeding 10% sea water and at a temperature greater than 19 C (66 F). In our experiments, survival of larvae at 19 C (66 F) after 6 days was 50% greater than survival of newly-hatched larvae at 18.5 C (65 F) from 2-hour-old fertilized eggs (Turner and Farley 1971). Evidently, 2-hour-old fertilized eggs are more vulnerable to increased salinities at higher temperatures than 1-day-old eggs. Furthermore, at salinities between 10 and 70% sea water, we obtained 25 to 32% better survival of 1-day-old larvae than with 1-day-old eggs (Table 1).

Different survival rates under identical salinities, as found between our experiments and those of other workers, could be due to differences in the ionic composition of the water. Turner and Farley (1971) showed that survival of striped bass eggs incubated in San Joaquin River water with a TDS of 623 ppm after getting mixed with natural estuarine water was 50% higher than in Tuolumne River water with a lower TDS of 525 ppm, but containing saline irrigation runoff water. Consequently, we regard the ionic composition of diluted sea water to be far more beneficial for the eggs and larvae than comparable fresh water with a high load of total dissolved solids.

We did not find any remarkable growth differences based on length of larvae reared up to 33 days in fresh water and those reared in different salinities (20, 40, and 60% sea water). Length measurements alone are an insufficient index for growth since they do not always reveal the weak and emanciated condition of larvae. Also, we observed that after the first week there was slight shrinkage of larvae in the higher salinities but not in fresh water, and this may have minimized the length differences. This is reflected in growth differences based on dry weight of larvae, because growth rate by weight in 60% sea water was 25% better than in lower salinities or even fresh water, although our best survival was in 40% sea water. Our results do not entirely agree with Bayless (1972) who found maximum growth in 40% sea water and best survival in 30% sea water over a period of 21 days, but he did not test growth in higher salinities. It appears that larvae survive better in low salinities but grow faster in higher salinities. Tolerance to higher salinities increases with age. Even though we recognize that food has a direct effect on growth, it was impossible for us to study this variable because the type of food and the concentration of food organisms available to the larvae in different salinities need to be standardized before exact differences in growth can be accounted for.

Our results show that striped bass fry can be reared in full sea water immediately after metamorphosis without obvious signs of stress behavior, for at least a period of 15 months. Even though our study indicated that the larvae can adjust to full sea water while undergoing metamorphosis, it was safer to transfer them after complete metamorphosis, when they were 33 to 35 days old. The average growth of 13 cm (5.2 inches) in 11 months and the maximum growth of 23.8 cm (9.5 inches) in 15 months in our experiments was approximately the same as Steven (1966) found in a natural population in California, but was 30% above the average first-year growth of 10 cm (4 inches) reported by Clark (1938).

The results of our study indicate that rearing of striped bass larvae in diluted sea water and the fry in sea water should ensure a better survival than found in freshwater hatcheries. The high rate of mortality of larvae reared in fresh water which continues even after metamorphosis has not occurred in our experiments with sea water. To overcome the difficulties encountered in rearing of striped bass larvae, we suggest a program of progressive increase in salinity to enhance survival and growth of striped bass larvae. To hatch eggs, only slightly brackish water, salinity not exceeding that of 10% sea water should be used. For larval rearing through metamorphosis the following regimes are best for growth and survival.

Optimal growth		*Optimal survival*	
Age	*Percent sea water*	*Age*	*Percent sea water*
Day 1 thru 9	20	Day 1 thru 6	10
Day 10 thru 19	40	Day 7 thru 13	20
Day 20 thru 29	60	Day 14 thru 20	40
Day 30 thru 35	80	Day 21 thru 29	60
Day 36	100	Day 30 thru 35	100

SUMMARY

Our study shows that diluted sea water is beneficial for rearing striped bass larvae and for hatching of eggs. Our results on salinity tolerance of striped bass eggs showed higher survival of larvae in salinities between 10 to 50% sea water than in fresh water. However, survival in these salinities was enhanced further by acclimating 1-day-old larvae instead of eggs.

Five-day-old larvae acclimated to salinities of 20, 40, and 60% sea water and reared up to 33 days of age, continued normal development through metamorphosis. Subsequent growth in higher salinities was faster than in fresh water, over a period of 4 weeks. The larvae in salt water looked healthier and better than those in fresh water.

Striped bass larvae were rapidly acclimated to full sea water within 1 month and reared successfully under laboratory conditions for a period of 15 months. Over this extended period of time, the average and maximum growth compared favorably with that found in natural waters. The larvae, if acclimated to full sea water before metamorphosis, did not survive. We found that the best time for the introduction of larvae to full sea water is just after metamorphosis.

ACKNOWLEDGMENTS

We are grateful to Alex Calhoun, former Chief, Inland Fisheries Branch, California Department of Fish and Game, for suggesting this problem. We also thank Frank Cochrane and Mas Yamashita for the supply of striped bass eggs produced at the Central Valleys Hatchery, Elk Grove; Richard L. Johnson for technical assistance; and Charles K. Barry for reviewing the manuscript.

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ESTIMATION OF THE EFFECTS OF ENVIRONMENTAL VARIATIONS ON THE EGGS AND LARVAE OF THE NORTHERN ANCHOVY

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ABSTRACT

Expanded studies of stock and recruitment at the Southwest Fisheries Center have led to additional objectives for laboratory and field work concerning the northern anchovy, *Engraulis mordax*. In addition to monitoring the stock size of the spawning portion of the anchovy population, we have begun to examine the possible causes and rates of larval mortality.

In this paper we show that the sampling effort required to measure changes in larval survival must be much greater than that used to monitor anchovy spawning biomass, i.e., closer intervals of sampling (in time and space) will be needed over relatively broad areas. Although existing sampling techniques are probably adequate to accomplish this, we show that there still remains the need to refine our statistical methods for analyzing larval age groups, data required for assigning larval mortality rates.

Changes in anchovy spawning are compared to seasonal and annual variations in sea water temperature, vertical temperature gradients, upwelling, California Current speed, flushing rate of the Southern California Bight, and secondary production. It appears that the usual habit of the anchovy to spawn in the southern California area in winter, alters radically in some years. The cause for this is not yet known. Quarterly apparent mortality rates are assembled for the years of greatest environmental changes in the southern California regions for anchovy eggs and larvae (to 6.25 mm).

New biological information needed for analyzing the causes of anchovy larval mortality has been assembled. For example, first feeding anchovy larvae require abundant food in a narrow size range and of particular species. *Gymnodinium splendens*, a naked dinoflagellate about 40 μm in diameter, supports growth when it occurs in concentrations of 20 or more cells per ml. Tests with laboratory reared larvae have confirmed the existence of suitable strata of larval food organisms in nearshore waters which are associated with chlorophyll maximum layers at 15–30 m depth. Storms were observed to disperse the food organisms until they were too low in number to support larval growth.

INTRODUCTION

Review of Field and Laboratory Research on California Anchovy, and the CalCOFI Program

In the last two decades (1955–1974) the northern anchovy, *Engraulis mordax*, supplanted the Pacific sardine, *Sardinops caerulea*, in biomass and in the commercial and live bait fisheries off the California coast (Baxter, 1967; Messersmith, 1969; Ahlstrom, 1966). The northern anchovy is now the chief forage fish for most of the large sport and commercial fishes of the California Current and represents a large, underutilized fishery resource, probably exceeding in biomass the former sardine population.

Estimates from a number of sources (see Messersmith, 1969, for a resume; Smith, 1972) agree that the standing stock of the northern anchovy off California and Baja California exceeded 4 million metric tons in the 1960's. This large population is the result of a rapid increase in numbers of anchovies since 1950 to 1951 when the population was estimated to be less than 1 million metric tons (Smith, 1972). This dramatic increase in numbers and biomass of the anchovy took place while the Pacific sardine population declined to a point where fishing was no longer profitable and when the standing stock of sardines was reaching a low point of less than 10,000 metric tons in 1965 (Smith, 1972) from which it had not recovered in the ensuing 8 years.

Loukashkin (1970) has shown that *E. mordax* is chiefly zooplanktivorous; thus, this large biomass of anchovies undoubtedly has had an impact on the food web, in particular on the secondary production and standing stock of zooplankton of the California Current. It also seems likely that the management of fisheries on the northern anchovy will be complicated by radical shifts in the success of year classes contributing to the fishery.

The fundamental objectives of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) program in the California Current region have been to measure the changes in biomass of the major pelagic fish populations inhabiting the region and to find explanations for these changes. Recent major reviews of the CalCOFI program including Marr (1960), Murphy (1966), Ahlstrom (1965, 1968), Smith (1972), and Soutar and Isaacs (1974) permit one to conclude that the major changes in the biomass of several populations in this region have been adequately monitored. In addition, it appears that changes in biomass which have been observed cannot yet be explained in terms of fishing effort, competition among species, or environmental variations.

Most changes in biomass of populations studied through monitoring a fishery appear to be due to changes in the success of recruitment to the fishable population. For example, spawning success varied independently of the spawning stock size of the sardine population by 7 times, from 1932 to 1957 (Murphy, 1966, p. 77). There is reason to believe similar changes occurred in spawning success of the anchovy (Soutar and Isaacs, 1974) during the last century.

In a renewed attempt to explain changes in biomass, we intend to examine the food requirements of the anchovy at all stages in its life cycle, to describe the incidence of suitable feeding areas in the ocean, and to discuss how changes in food requirements and feeding might affect recruitment. Where it is applicable, suggestions are made to change present sampling programs in order to provide additional information for evaluating changes in the environment as these might induce changes in the anchovy population, e.g., changes in growth rate, mortality, and fecundity. Because of the existence of considerable information on food requirements at the larval stage, and records of larvae from most of the northern anchovy spawning area since 1951, we have chosen to describe in detail the parameters which seem necessary for estimating the effects of environmental variations on survival and growth of anchovy eggs and larvae. We anticipate this will guide future workers who may need to establish similar criteria for studying biomass fluctuations in other fish populations.

ASSESSMENT OF ANCHOVY EGGS AND LARVAE AND ITS RELATIONSHIP TO THE SPAWNING BIOMASS

The amount of effort required for the efficient assessment of eggs and larvae is different when the objective is to monitor the size of the spawning stock than when the objective is to analyze mortality which occurs during the planktonic phase of a fish's life cycle. The surveys now being conducted in CalCOFI have been designed to monitor the spawning biomass. Estimates of mortality require more precise sampling and the evaluation of some major biases. It is the purpose of the following to define sampling requirements for each of these objectives from the long data record from CalCOFI surveys, and from some intensive investigations of local sampling variability.

Pelagic Pattern

The chief obstacle to effective sampling is the intensity of adult anchovy schooling behavior when spawning. In areas where spawning is taking place, newly spawned eggs at densities of hundreds per square meter may be within a few hundred meters of areas where there are no eggs at all. Dispersal of these eggs from the spawning sites is apparently very slow, with identifiable traces of this pattern persisting for the entire time that the larvae are

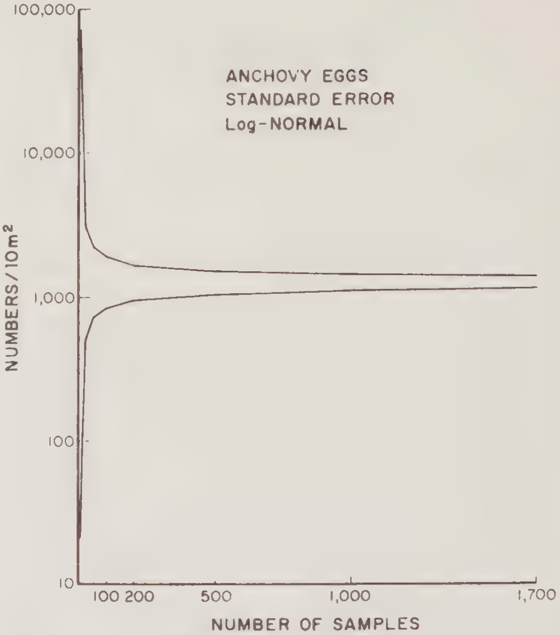

FIGURE 1. The relationship between standard error and number of samples for anchovy eggs using a log-normal transformation. Single sample variability at the origin indicates the intensity of patchiness.

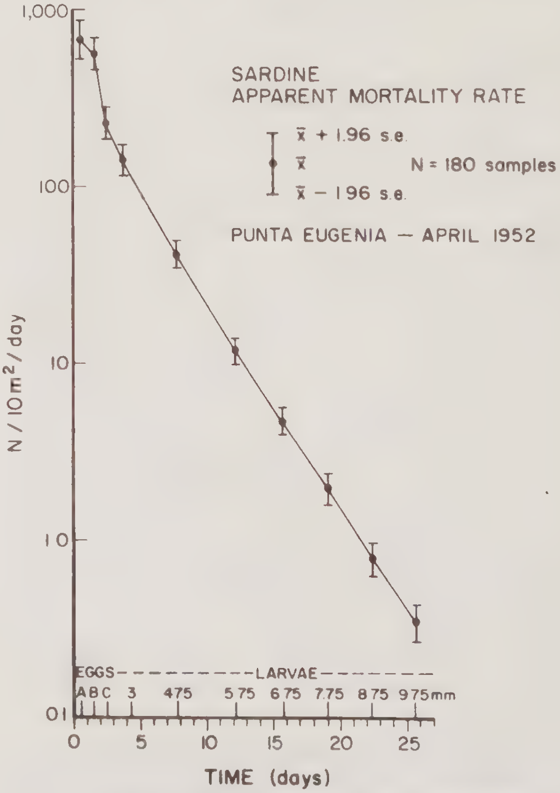

FIGURE 2. Apparent mortality rate of Pacific sardine eggs and larvae, N = 180.

vulnerable to the net. It seems likely that schooling behavior begins before the larvae have been entirely dispersed from the schooling behavior of the adults.

Regardless of the cause of pelagic pattern, the effect on sample precision must be overcome for the purposes of estimating the amount of spawning and determining the fate of the spawn. Precision may be increased by increasing the sampling effort and maintaining a rigorous sampling quality control. This is particularly important in the sampling of log-normal distributions common in the sea. For 10% sample confidence limits, when eggs are sampled, about 500 samples per space-time unit (Figure 1) need to be collected. To obtain a 25% sample confidence limit, which is adequate for determining rapid mortality rates (Figure 2), fewer than 100 samples may suffice (Figure 3). Satisfactory results in monitoring spawning biomass have been obtained in CalCOFI using as few as 30 samples per space-time unit.

For estimation of spawning, the most important bias is due to the loss of eggs and small larvae through the meshes of the plankton net. Lenarz (1952) found that a few paired tows of nets with different meshes are adequate for quantifying this bias. For determining the fate of the spawn, the most important bias is the growing tendency of larvae to avoid the net. No suitable solution is now available for this avoidance problem (Clutter and Anraku, 1968) but bongo nets and other higher speed bridle-free nets can materially increase the number of larger larvae collected.

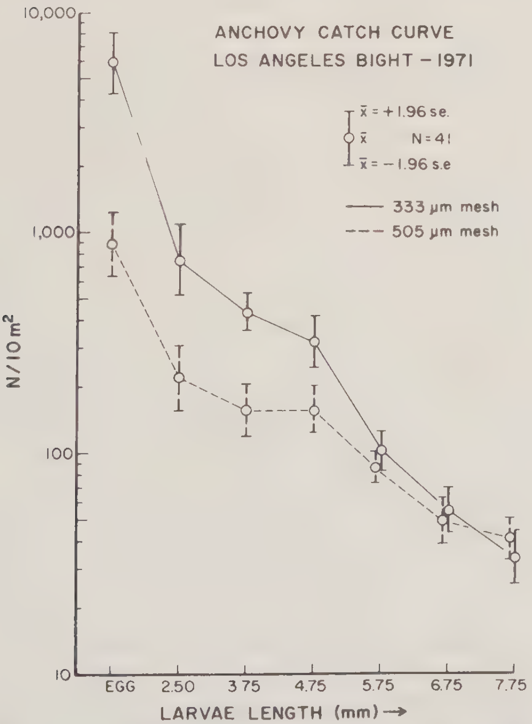

FIGURE 3. An example of the discrimination between the catch of anchovy eggs and larvae using two net meshes, N = 41.

The issue of assigning confidence limits to data derived from counts of eggs and larvae of pelagic fish has rarely been treated satisfactorily (Bagenal, 1955; Harding and Talbot, 1973). Among the pressing problems is evaluating mortality rates between two adjacent age classes when the variance of the number of fish in each age class is changing and the older class has been dispersed over a wider area than the younger class. While analysis of the existence of a difference can be attempted using log-transformed data, estimating the magnitude of the difference must be accomplished using the original arithmetic means. As pointed out by Cassie (1968, p. 109), "means obtained from log-transformed data are, after taking anti-logarithms, geometric means which will be smaller than the corresponding arithmetic means." Observations containing small and uniform proportions of "O" observations are satisfactorily treated in logarithmic transformations by adding a constant to each value, usually "1". However, in larval sampling, there are trends in the proportion of "O" observations. Therefore, the standard practice of adding "1" and taking the logarithm is not applied because it has not been adequately studied under these conditions.

Seasonal and Annual Changes in Spawning, Environmental Parameters, and Apparent Larval Mortality

A sample of existing data has been assembled to illustrate the magnitude and timing of spawning and other seasonal events as well as examples of changes between years. These seasonal and annual changes may be used as guides to design improved surveys and devise analytical techniques for the assessment of larval mortality and some of its causes. The area and time period chosen for these examples is the Southern California Inshore or SCI (Smith, 1972) for the years 1953 through 1960. This area was chosen because it was sampled thoroughly and regularly. The time interval was chosen to span two unusual climatic events; in 1956 the ocean off southern California was colder than average and in 1958 it was warmer than average.

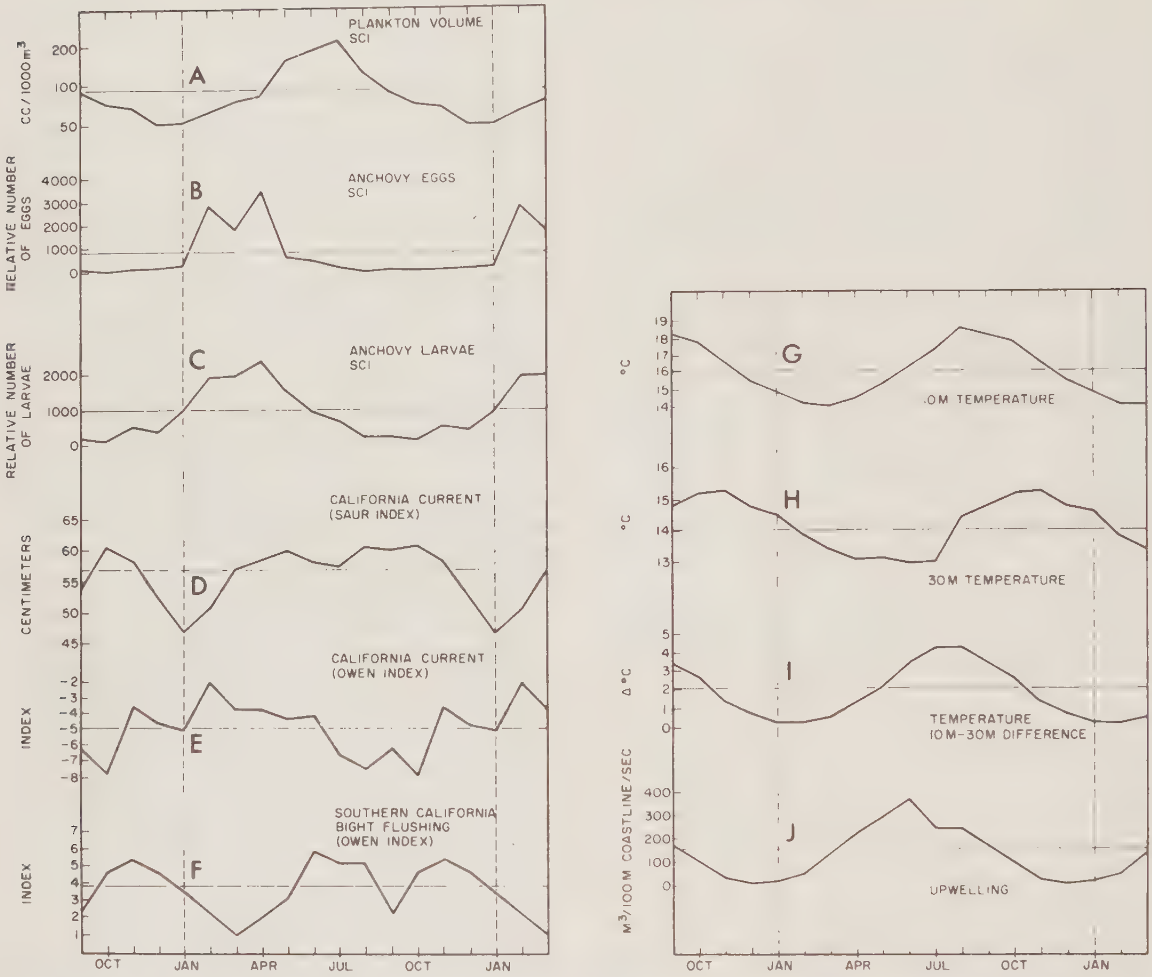

FIGURE 4. Average annual cycles (1953–1960) in the Southern California Inshore region. Six months are repeated for cycle emphasis; a) plankton volume, b) anchovy eggs, c) anchovy larvae, d) the California Current (Saur, 1972), e) the California Current south of Pt. Conception within the CalCOFI grid (Owen, National Marine Fisheries Service, La Jolla, Pers. comm.), f) Southern California Bight Flushing Index (Owen, National Marine Fisheries Service, La Jolla, pers. comm.), g) 10-meter temperatures, h) 30-meter temperatures, i) temperature difference between 10 and 30 meters, j) upwelling (Bakun, 1973).

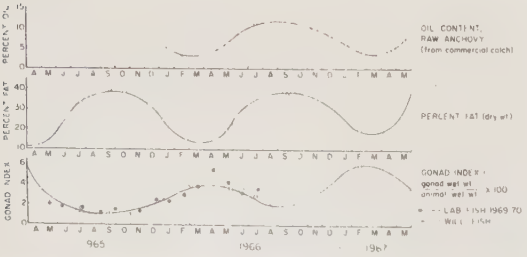

FIGURE 5. Annual northern anchovy fat and gonad cycles for 1965–1967. Oil content is from the commercial catch in California (data provided by Roland Finch, National Marine Fisheries Service, Terminal Island). Laboratory fish were kept in an outdoor pool at the La Jolla Laboratory of the Southwest Fisheries Center under ambient light and temperature conditions.

The seasonal maxima of anchovy spawning in the Southern California Inshore region appear to be in February, March, and April. The minima are in August, September, and October (Figures 4B, C). Maximum spawning coincides with the minimum temperature at 10 m depth. The temperature at 30 m decreases after the spawning maximum and coincides with upwelling (Bakun, 1973) which reaches a peak in June. Anchovy spawning also coincides with the maximum rate of increase in the 1953 to 1960 upwelling index. The lowest zooplankton standing stock is coincidental with the upwelling minimum in December although the zooplankton peak in July appears 1 month after the upwelling maximum. The fastest rate of increase in fat content of anchovy adults coincides with the zooplankton maximum (Figures 4A and 5). Average conditions for California Current strength by sea level difference approximations (Saur, 1972) and by geostrophic calculations (Owen, National Marine Fisheries Service, La Jolla, pers. comm.) do not agree closely (Figures 4D, E). Exchange of water between the rather permanent eddy in the Southern California Inshore region and the California Current (Owen's Southern California Bight Flushing Index, Figure 4F) appears to be at a minimum during the height of anchovy spawning. This indicates that water and spawned eggs and larvae are moving out of the Southern California Inshore region at a relatively slow rate. An 8 year average of each environmental and biological variable was calculated (Figures 4A–J and 5).

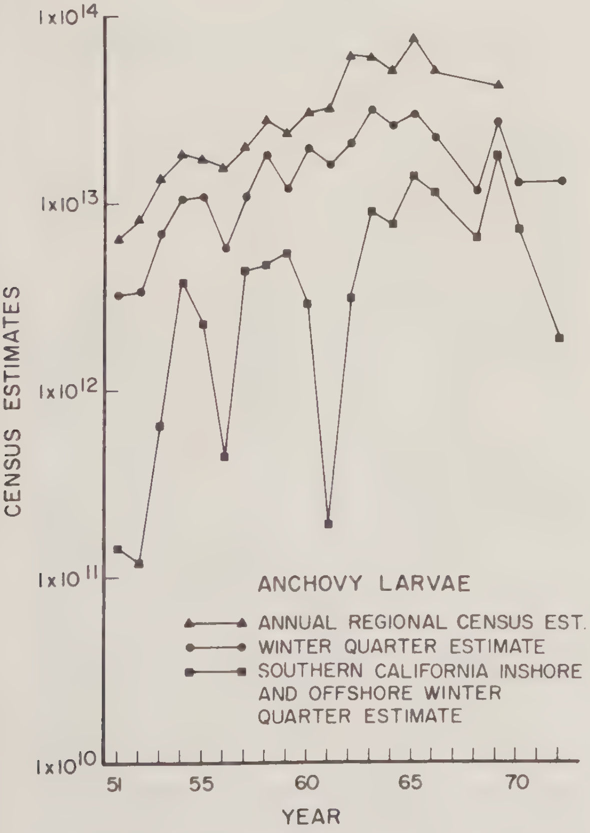

FIGURE 6. Time series of regional census estimates of anchovy larvae (Smith, 1972).

Five additional time series have been selected to illustrate the magnitude and extent of coincidence of annual variations in spawning and other routinely measured environmental data. Three curves represent the abundance of anchovy larvae (Figure 6). The increase in estimates of the abundance of larvae appears to be rather gradual in the annual census estimate for all anchovy larvae in the entire California Current sampling grid in all seasons. There is an increase in the total abundance of larvae in the winter quarter generally parallel to the annual estimates. The abundance of anchovy larvae in the winter quarter in both the Southern California Inshore and Offshore regions indicate this is a major spawning area for anchovy (Figure 6). The considerable changes in the fraction of the total larval population in these combined regions in this season suggest that studies of survival will need to be conducted over an even bigger area than the 35,000 square nautical miles represented.

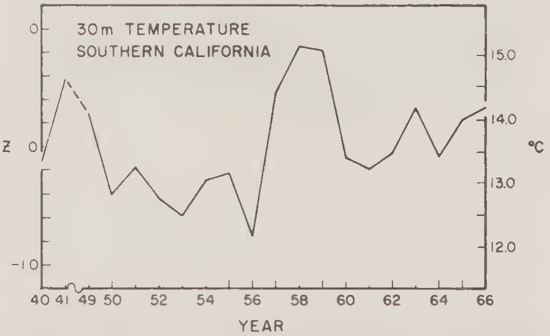

FIGURE 7. Thirty (30) meter annual average temperature for the Southern California Inshore zone, Z is the normalized standard deviation of the variable.

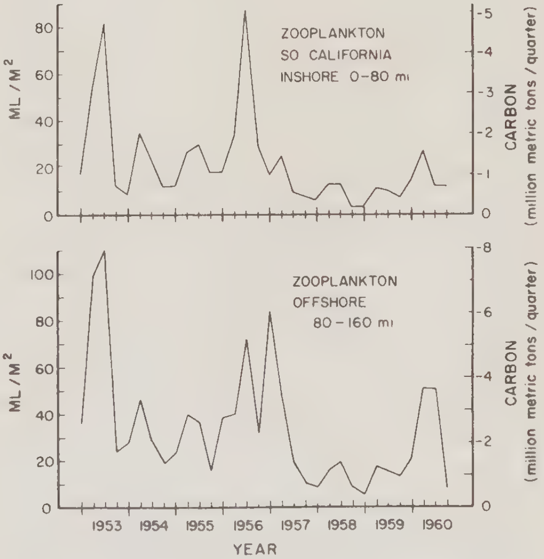

FIGURE 8. Zooplankton volumes, 1953–1960 for Southern California Inshore and Offshore regions. Carbon equivalents were obtained by multiplying wet volume figures by 0.056 (Cushing, 1971).

The time series of temperature at 30 m depth illustrates major climatic shifts in the Southern California Inshore region (Figure 7). Yet there does not appear to be any obvious direct control exerted by temperature over spawning. Lastly, two curves illustrate Southern California Inshore and Offshore zooplankton standing crop as well as estimates of secondary production by the "Cushing" method (1971) over the same reference period (Figure 8). Estimates of zooplankton production do not offer obvious explanations for major shifts in the amount or location of spawing. We conclude from these time series that over gross areas, changes in temperature and zooplankton production do not offer promising leads for finding cause and effect mechanisms which determine survival of larvae and recruitment to the parent stock.

Mortality rates for larvae in the sea are of special interest because these are needed to measure the effects of environmental variations on recruitment. These rates are difficult to derive because there have been few attempts to assign ages to the various size categories of larvae in our samples (Ahlstrom, 1954). Hatching time, however, is a function of temperature and as a first approximation, the ratio of hatching time at ambient temperature to that at 15°C has been used to adjust each egg and larval count. The regional census estimates of the eggs and various sizes of anchovy larvae have been assembled from the adjusted data. The numbers of eggs and larvae also have been corrected for an escapement bias described by Lenarz (1972). Quarterly estimates of egg and larval abundance in the Southern California Inshore region have been made (Table 1). The parameters of the least squares fit made to the simple exponential equation:

$$N_t = N_o e^{-zt}$$

where:

N_t = is an estimate of the number of eggs or larvae at time "t" in days

N_o = is the ln N at time zero, and

z = is the instantaneous rate of apparent mortality.

TABLE 1

Larval anchovy mortality rate by quarter (QTR) for each year (YR), 1953 to 1960.*

YR-QTR	Eggs	2.50 mm larvae	3.75 mm larvae	4.75 mm larvae	5.75 mm larvae	r_1	r_2	z_1	$(N_0)_1$	z_2	$(N_0)_2$
	1.5 days old	3.8 days old	5.6 days old	7.5 days old	9.8 days old						
53–1	1328	536	195	80	65	–.949	–.975	.3538	7.3889	0.3870	7.6431
2	355	201	83	47	15	–.996	–.993	.4188	6.8694	.3824	6.5866
3	493	1951	406	431	191	–.904	–.619	.3407	8.4987	.1623	7.1354
4	787	3197	1426	661	279	–.999	–.622	.4034	9.5563	.1755	7.8147
54–1	2482	3718	1725	964	462	–.997	–.902	.3408	9.4441	.2294	8.5927
2	2560	1494	256	133	61	–.957	–.976	.5046	8.8311	.4820	8.6584
3	3420	1585	434	264	129	–.969	–.985	.3964	8.6142	.4081	8.7040
4	475	500	193	84	39	–.994	–.962	.4216	7.7061	.3307	7.0116
55–1	3679	1707	1251	649	330	–.994	–.997	.2808	8.5859	.2854	8.6208
2	1879	1079	671	321	170	–.997	–.997	.3140	8.1948	.2954	8.0534
3	312	2461	597	307	170	–.961	–.486	.4273	9.1169	.1545	7.0320
4	187	86	137	36	21	–.866	–.913	.2829	5.8879	.2596	5.7106
56–1	1627	102	154	31	19	–.882	–.927	.3355	6.2490	.5001	7.5068
2	4631	2321	828	318	166	–.987	–.992	.4392	9.2664	.4225	9.1390
3	597	188	162	204	148	–.467	–.773	.0261	5.3340	.1356	6.1709
4	598	130	70	62	27	–.973	–.957	.2433	5.7584	.3432	6.5214
57–1	34741	3147	1989	1220	338	–.979	–.960	.3643	9.5757	.5067	10.6639
2	25402	5608	2050	1108	592	–.983	–.979	.3644	9.8443	.4488	10.4889
3	685	1721	382	200	137	–.934	–.824	.4030	8.5926	.2574	7.4798
4	1001	58	98	100	47	–.271	–.743	.0397	4.5401	.2821	6.3925
58–1	9668	3746	2044	760	376	–.995	–.997	.3933	9.7277	.3972	9.7573
2	3540	3627	1329	827	495	–.971	–.960	.3183	9.2015	.2632	8.7803
3	84	396	189	156	80	–.978	–.231	.2489	6.8242	.0472	5.2831
4	793	255	25	11	10	–.874	–.941	.5098	6.7669	.5771	7.2808
59–1	2227	1345	1103	207	93	–.967	–.959	.4856	9.2588	.4035	8.6317
2	3269	1581	1058	702	434	–1.000	–.995	.2143	8.1694	.2387	8.3558
3	41	372	87	41	21	–.968	–.487	.4621	7.3690	.1663	5.1092
4	196	398	97	19	8	–.984	–.906	.6609	8.3060	.4576	6.7524
60–1	1957	2411	948	390	186	–.993	–.945	.4259	9.3003	.3178	8.4747
2	6846	1172	757	532	293	–.998	–.945	.2262	7.9225	.3508	8.8747
3	127	247	75	76	37	–.923	–.804	.2811	6.3177	.1761	5.5153
4	53	48	6	5	1	–.955	–.956	.5867	5.7329	.4986	5.0596
n	32	32	32	32	32						
$\bar{x}$	3626	1481	651	342	170	–.995	–.997	.3550	8.5562	.3722	8.6876
s	7351	1416	653	346	165						

* Low values of z_1 and z_2 indicate high survival or low mortality; high values, the opposite. The intercept, N_0, is an *index* of the size of the spawning population, proportional to the logarithm of the amount of spawning which took place in each quarter No extrapolation nor prediction should be conducted from these slopes and intercepts without refitting curves with non-linear least squares; for example, the Marquardt algorithm or equivalent

r_1, z_1 and $(N_0)_1$ = without eggs

r_2, z_2 and $(N_0)_2$ = with eggs.

Sample values for eggs and larval lengths through 6.25 mm and the age of each stage are listed (Table 1). Parameter estimates r_1, z_1, and $(N_0)_1$ exclude the egg sample variable whereas r_2, z_2, and $(N_0)_2$ include the variable. One may see from the correlation coefficient, r, that the simple exponential model more effectively describes the sample data at the height of spawning in winter and spring quarters than in the summer and fall quarters. The sample variation is better described when the egg census estimate data are omitted. From the tabular summary, it is evident that the number of eggs from sample to sample varied proportionately more than did the larvae.

BASE REQUIREMENTS FOR FEEDING, GROWTH, AND SURVIVAL OF ANCHOVY LARVAE

Numbers of research papers have appeared from the Southwest Fisheries Center, La Jolla, California, which developed criteria for growth and survival of anchovy larvae (Hunter, 1972; Hunter and Thomas, 1974; Kramer and Zweifel, 1970; Lasker, 1964; Lasker et al., 1970; Lasker, 1975; O'Connell and Raymond, 1970; Theilacker and Lasker, 1974; Theilacker and McMaster, 1971; Thomas, Dodson and Linden, 1973).

Feeding of larvae in relation to biological and physical environmental conditions has been the main area of investigation in order to examine the hypothesis that variations in year class strength are probably due to differential mortality of larvae when they first begin to feed; i.e., that a lack of food at the time of first-feeding may be the main cause of huge mortalities and result in small year classes (Hjort, 1914).

The northern anchovy has been and can be continually matured sexually and spawned in captivity at the Southwest Fisheries Center (Leong, 1971) which provides investigators with ample eggs and larvae for experimental work. Some of the studies referenced above have been done with laboratory produced larvae. These investigations have shown us that the following criteria need to be met for reasonable success in laboratory survival and growth of *Engraulis mordax* larvae. Another discussion of these criteria may be found in Lasker (1975).

The size of the food particle at first-feeding must neither be too small nor too large. Berner (1959) examined stomach contents of northern anchovy larvae from field collections and found that particles of food in the intestines of first-feeding larvae ranged from 24 to 186 μm long. However, over 70% of the food was between 60 and 80 μm long. This seems to be controlled by the mouth gape of the larva as borne out by laboratory feeding studies. Algal cells between 10 and 20 μm in diameter are not eaten by first-feeding anchovy larvae while particles of 40 μm and larger are eaten without difficulty. Organisms the size of the rotifer *Brachionus plicatilis,* which range from 99 to 281 μm long and 66 to 182 μm wide can be taken by a small proportion of first-feeding anchovy larvae (Theilacker and McMaster, 1971; Hunger, 1972).

The number of food particles per unit volume in the first-feeding anchovy's environment must be above a minimum concentration. O'Connell and Raymond (1970) showed that a minimum density of micronauplii (about 1/ml) was needed for anchovy larvae to survive in laboratory experiments. Hunter (1972) has shown that there is a minimum density of algal cells that must be present if an anchovy larva is to obtain enough nutrients for metabolism, but his calculation is about 10X lower than the minimum number of cells we find to be necessary (i.e., about 20 to 40 cells/ml) for metabolism, growth, and to account for capture inefficiency in the laboratory.

Not all food organisms capable of being eaten by anchovy larvae support growth and survival. In the laboratory only one phytoplankter, *Gymnodinium splendens,* of a number tested, suppported growth of first-feeding anchovy larvae. However, larvae fed a variety of foods, such as found in wild plankton, invariably grow faster and survive better than those fed single species of organisms in the laboratory, but only when the plankton was concentrated to increase the density of the food organisms per unit volume (Kramer and Zweifel, 1970). Hunter (1972), who analyzed Arthur's (1956) data, pointed out that phytoplankton comprises at least 32% of the diet of first-feeding anchovy larvae. We know from rearing experiments that some nauplii (e.g. from the harpacticoid copepod *Tisbe furcata;* Hunter, National Marine Fisheries Service, La Jolla, unpublished) support good growth in first-feeding larvae, while other invertebrate larvae do not (Lasker et al., 1970).

The frequency of feeding strikes, and thus the success in capturing food is greater with high densities of food organisms. Hunter (1972) showed that feeding success at first-feeding for anchovy larvae is only about 10% of the feeding strikes made. Recently, Hunter and Thomas (1974) studied the feeding behavior of anchovy larvae in patches of *Gymondinium splendens* and found that the larvae fed more frequently inside the patch than outside. This differential feeding was related to the density of the food organisms in the larva's area.

Recent Observations at Sea

Lasker (1975) used first-feeding anchovy larvae produced by laboratory spawned fish to detect concentrations of larval fish food *in situ* along the California coast. First-feeding larval anchovies, whose development was controlled by temperature manipulation aboard ship, were placed in samples of Southern California Bight water taken from the surface and from chlorophyll maximum layers, usually 15 to 30 m below the surface. Feeding by larvae in water from the surface was minimal in all experiments but extensive feeding occurred in water from the chlorophyll maximum layers when these contained phytoplankters having minimum diameters of approximately 40 μm and which occurred in densities of 20 to 400 particles/ml. In March and April 1974, the chlorophyll maximum layer along the California coast from Malibu to San Onofre (a distance of about 100 km) consisted chiefly of a bloom of the naked dinoflagellate *Gymnodinium splendens,* a food organism known to support growth in anchovy larvae. Copepod nauplii and nonliving particles were never in high enough concentration or of the proper size to be eaten by the larvae. A storm which caused extensive mixing of the top 20 m of water obliterated the chlorophyll maximum layer and effectively destroyed this feeding ground for larval anchovy.

ADULT PHYSIOLOGY

Lenarz and Hunter (National Marine Fisheries Service, La Jolla, pers. comm.) have demonstrated that there is a distinct seasonal trend in anchovy egg size and that the size of larvae at 3 days of age is related to the original egg size. Whether smaller larvae are at a disadvantage in the sea is not known but knowledge of when adults spawn is probably essential information in later studies of recruitment.

We know also from MacCall (California Department of Fish and Game, La Jolla, pers. comm.) that the apparent mortality rate of adults from the southern subpopulation (see below) is higher than that of the central subpopulation. These examples have prompted us to examine some pertinent features of cyclic phenomena in the physiology of the adult northern anchovy.

Subpopulations

Unpublished work by Vrooman and Paloma (MS)[1] gives good immunological evidence for the existence of three distinct subpopulations of the northern anchovy off the west coast of the United States and Baja California, Mexico. Presumably, these reproductively separate races do not interbreed. One population is centered chiefly off lower Baja California, another, the so-called central subpopulation which contains the major portion of the stock, ranges from northern Sebastian Vizcaino Bay, Baja California, to San Francisco, California, while a northern subpopulation extends from San Francisco to at least Newport, Oregon. A considerable amount of information is available on the year class strength and biomass of the central California subpopulation (Vrooman and Smith, 1971; Smith, 1972; Soutar and Isaacs, 1974).

Lasker (1970) showed that there is a reciprocal relationship between the amount of fat in the body of the Pacific sardine, *Sardinops sagax caerulea,* and the maturation of the gonad, as measured by the gonad index (i.e. wet weight of the gonad divided by the wet weight of the fish X100). Shul'man (1960) in his review on lipids in fish stated that this is to be expected in most temperate fish. The same kind of relationship exists in the northern anchovy (Figure 5). Note that oil extracted from the commercial catch also reflects this cyclic phenomenon. We have also plotted mean gonad indices from anchovies kept in an outdoor tank at the La Jolla Laboratory. All of the fish came from the central subpopulation. Lipid deposition reaches a maximum in the anchovy during the summer, and a minimum during the peak of the spawning season (February, March, and April).

Laboratory experiments (Leong, 1971) have shown that northern anchovy gonad maturation can be induced by exaggerating winter light conditions. For example, 4 hours of light and 20 hours of darkness insures maintenance of high gonad indices (i.e. GI = 5% or higher) for as long as this light regime is maintained. Thus, this winter-early spring spawning fish's reproductive activity seems keyed to the seasonal light regime.

LARVAL ANCHOVY SURVIVAL

Recent work by Lasker (1975) has shown a correlation between the vertical stratification of suitablysized phytoplankters and the appearance of first-feeding anchovy larvae. The importance of the extent of these phytoplankton stratified patches, both horizontally and vertically, cannot be overestimated. We believe that virtually all survival of first-feeding anchovy larvae is linked to these favorable areas.

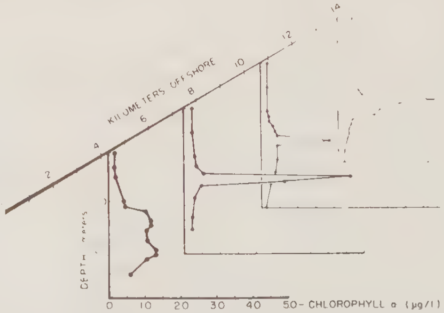

Figure 9. Chlorophyll maximum layer in an offshore transect at a right angle to the shore at San Onofre, California, April 22-23, 1974. The chief component of the layer was a 10 μm diameter green flagellate (Lasker, 1975).

Two examples of vertical and horizontal structure of phytoplankton patches, one taken in April 1974 and the other in October 1974 off San Onofre, California, were obtained (Figures 9 and 10). Results emphasize the vertical distribution of a 10 μm green flagellate (Figure 9) and the horizontal, vertical, and size distribution of a patch characterized by a 30 to

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[1] Vrooman, Andrew M. and Pedro A. Paloma. MS. Subpopulations of northern anchovy *Engraulis mordax* Girard.

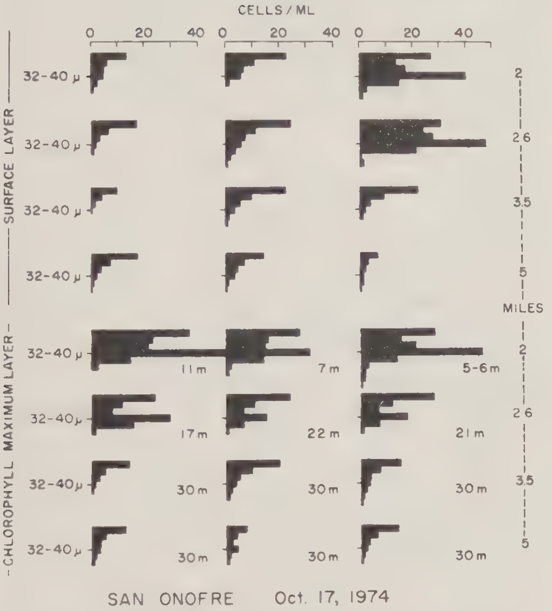

Figure 10. Particle size distribution from 12 adjacent stations off San Onofre, California, October 17, 1974. Five size groups are shown in histograms for each station; these are, top 16–20 µm, followed by 20–25 µm, 25–32 µm, 32–40 µm, 40–50 µm, and 50–64 µm.

40 µm dinoflagellate, *Gonyaulax polyedra* (Figure 10).

Quantitative studies of the food requirements of larvae and the feeding capability of predators on larvae (Hunter, 1972; Lillelund and Lasker, 1971; Theilacker and Lasker, 1974) indicate that average conditions in the sea are insufficient in food supply and sufficient predatory capability exists to consume the entire spawn. We have seen above that spatial patterns in the vertical and horizontal planes results in nursery patches for first-feeding anchovy larvae. Cursory examination of the patchy distribution of predatory organisms such as euphausiids and chaetognaths indicates that most of the predatory capability is concentrated in a relatively small proportion of the ocean, thus the spaces between patches of predators serve as a refuge for the survival of sufficient numbers of larvae for maintenance of population. The major criteria for survival of larvae appears to be related to coincidence rather than abundance alone; that is, a patch of larvae will survive if it coincides with an adequate patch of food organisms and also if it does not coincide with a patch of predators adequate to destroy the larval patch. These conditions also lead one to infer that the major influences on larval survival depend not on adequate production alone, but a stable oceanographic environment which will permit and maintain a discrete pattern of distribution of larval food, larvae, and the predators on larvae.

ACKNOWLEDGMENTS

This work was supported in part by a grant from the Brookhaven National Laboratory of the Energy Research and Development Administration (ERDA). This is MARMAP (Marine Resources Monitoring, Assessment and Prediction) Contribution No. 134.

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7730

SEASONAL MIGRATION OF NORTH PACIFIC ALBACORE, *THUNNUS ALALUNGA*, INTO NORTH AMERICAN COASTAL WATERS: DISTRIBUTION, RELATIVE ABUNDANCE, AND ASSOCIATION WITH TRANSITION ZONE WATERS

R. Michael Laurs and Ronald J. Lynn[1]

ABSTRACT

In the spring months of 1972-74, fishery-oceanography surveys were conducted in the eastern North Pacific which combined intensive oceanographic sampling by research vessels with concurrent fishing effort for albacore by chartered commercial fishing vessels. The catches demonstrate an association of albacore distribution with the Transition Zone and its boundaries. The relative abundance of albacore was found to be high in the eastern sector of the Transition Zone or a period just prior to their movement across the California Current and into the traditional nearshore fishing grounds. These centers of high relative abundance of albacore are sometimes sufficient to support commercial fishing earlier and farther offshore than the traditional fishing season. Variations in the pattern of migration occur in apparent response to variations in the character and development of the Transition Zone and its frontal structure. Analyses of albacore tagging and size frequency data provide evidence that the shoreward-migrating albacore of the Pacific Northwest and California are independent groups.

The North Pacific albacore, *Thunnus alalunga* (Bonnaterre), is a wide-ranging species which spawns in the central subtropical Pacific, performs transpacific migrations, and supports important commercial fisheries in the western, central, and eastern North Pacific. That marked variations in distribution and relative abundance of albacore occur in the eastern North Pacific is indicated by major latitudinal shifts in the location of the U.S. fishery off the west coast of North America (Laurs et al. 1976). In order to evaluate factors which may affect variations in distribution, relative abundance, and migration patterns of albacore in the eastern North Pacific, and to improve our understanding of the underlying factors affecting the onset and subsequent development of the fishery, early season surveys were conducted in offshore waters of the North American Pacific coast in 1972-74.[2] These surveys found that relative abundance of albacore was high in the vicinity of oceanic fronts of the Transition Zone waters in the eastern North Pacific. Survey results also provide the basis for a hypothesis concerning migration of albacore into coastal waters off the west coast of North America. During these surveys albacore were taken in commercial concentrations farther offshore than traditionally, and several weeks earlier than the fishing season which usually commences in mid-July.

BACKGROUND INFORMATION

Numerous exploratory albacore fishing and albacore oceanographic surveys have been conducted in the central and eastern North Pacific. From surveys conducted during the 1950's, scientists described seasonal variations in distribution of albacore in the central and parts of the eastern Pacific, and demonstrated the association of albacore with Transition Zone waters in the central North Pacific (Shomura and Otsu 1956; Graham 1957; McGary et al. 1961). Flittner (1963, 1964) reported on albacore trolling experiments conducted from U.S. Navy picket vessels operating approximately along long. 130° to 135°W, and presented a schematic model of albacore movement off the Pacific coast (Flittner 1963). Neave and Hanavan (1960) showed that the northern limit of albacore catches made during high-seas salmon gillnetting studies conducted between long. 125° and 175°W was about lat. 45° to 47°N in July and

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[2] These surveys were carried on cooperatively by the National Marine Fisheries Service, Southwest Fisheries Center La Jolla Laboratory, and the U.S. albacore fishing industry through the American Fishermen's Research Foundation.

Manuscript accepted February 1977.
FISHERY BULLETIN: VOL. 75, NO. 4, 1977.

lat. 45° to 50°N in August and September. According to Brock (1943), yachts sailing between Hawaii and Oregon during June made albacore catches between lat. 30° and 44°N in waters between long. 154° and 140°W.

Numerous exploratory fishing and oceanographic surveys also have been conducted within a few hundred miles of the coast to obtain information on distribution, availability, and migration patterns of albacore during early season in waters off the Pacific Northwest (Powell 1950, 1957; Powell and Hildebrand 1950; Powell et al. 1952; Schaefers 1953; Owen 1968; Meehan and Hreha 1969; Pearcy and Mueller 1970; and others), and in waters off California (Graham 1959; Clemens 1961; Craig and Graham 1961; and others listed in Clemens 1961 and Pinkas 1963). Johnson (1962), Laurs et al. (1976), and others have discussed variations in distribution and relative abundance of albacore in waters off North America where the U.S. fishery takes place. These studies have shown: 1) the limits of where albacore are found; 2) their general migration patterns; 3) the importance of environmental conditions and changes, notably ocean temperature, in relation to the distribution and relative abundance of albacore; and 4) the considerable annual variation in location of available concentrations of albacore.

In the present study early season albacore surveys were planned to encompass a portion of the eastern sector of the Transition Zone during a period prior to the commencement of the nearshore fishery. The primary objectives of these surveys were:

1) To investigate the early season distribution and abundance of albacore off the North American Pacific coast.
2) To investigate the eastward migration path of albacore entering the American west coast fishery.
3) To determine if migrating albacore are associated with major offshore oceanographic features, particularly the Transition Zone and the ocean fronts that form its boundaries.

METHODS

The general work plan for each offshore survey employed one National Marine Fisheries Service (NMFS) research vessel (*Townsend Cromwell* in 1972 and *David Starr Jordan* in 1973 and 1974) and a group of 5 to 12 commercial albacore fishing vessels on charter to the American Fishermen's Research Foundation (AFRF). The research vessel and chartered fishing vessels worked cooperatively to obtain estimates of distribution and relative abundance of albacore in the offshore area and to make concurrent oceanographic measurements. The research vessel collected physical, chemical, and biological oceanographic data and conducted supplementary fishing activities. The fishing vessels conducted exploratory fishing, tagged fish, and collected surface and subsurface temperature data. The oceanographic findings made on meridional transects were used in directing the exploratory fishing operations, particularly at the onset of each survey. In several instances, especially in 1973 and 1974, the findings of large numbers of fish were used to redirect the research vessel to conduct detailed oceanographic observations in the vicinity.

Operations Aboard Research Vessels

Three meridional oceanographic sections were taken along long. 135°, 137°30′, and 140°W between lat. 31° and 41°N in 1972 and 1973; in 1974 the middle section, portions of the section along long. 135°W, and additional transects were taken (Figure 1). Hydrographic stations were occupied at 25- to 30-n.mi. intervals. Figure 2 shows station positions occupied in 1973; Lynn and Laurs[3,4] gave figures of the station positions for other years. Observations included: 1) salinity-temperature-depth profiles to 500 or 1,000 m using an STD;[5] 2) Nansen bottle or command rosette sampler[6] bottle casts for collection of water samples for determination of dissolved oxygen, chlorophyll, and salinity; 3) oblique zooplankton net hauls and simultaneous surface hauls with neuston plankton nets; and 4) at night stations,

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[3] Lynn, R. J., and R. M. Laurs. 1972. Study of the offshore distribution and availability of albacore and the migration routes followed by albacore tuna into North American waters. *In* Report of joint National Marine Fisheries Service-American Fishermen's Research Foundation albacore studies conducted during 1972, p. 10-44. (Unpubl. rep.)

[4] Lynn, R. J., and R. M. Laurs. 1973. Further examination of the offshore distribution and availability of albacore and migration routes followed by albacore into North American waters. *In* Report of joint National Marine Fisheries Service-American Fishermen's Research Foundation albacore studies conducted during 1973, p. 3-35. (Unpubl. rep.)

[5] Plessey model 9006 electronic salinity-temperature-depth profiler. Use of a trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.

[6] General Oceanics, Inc.

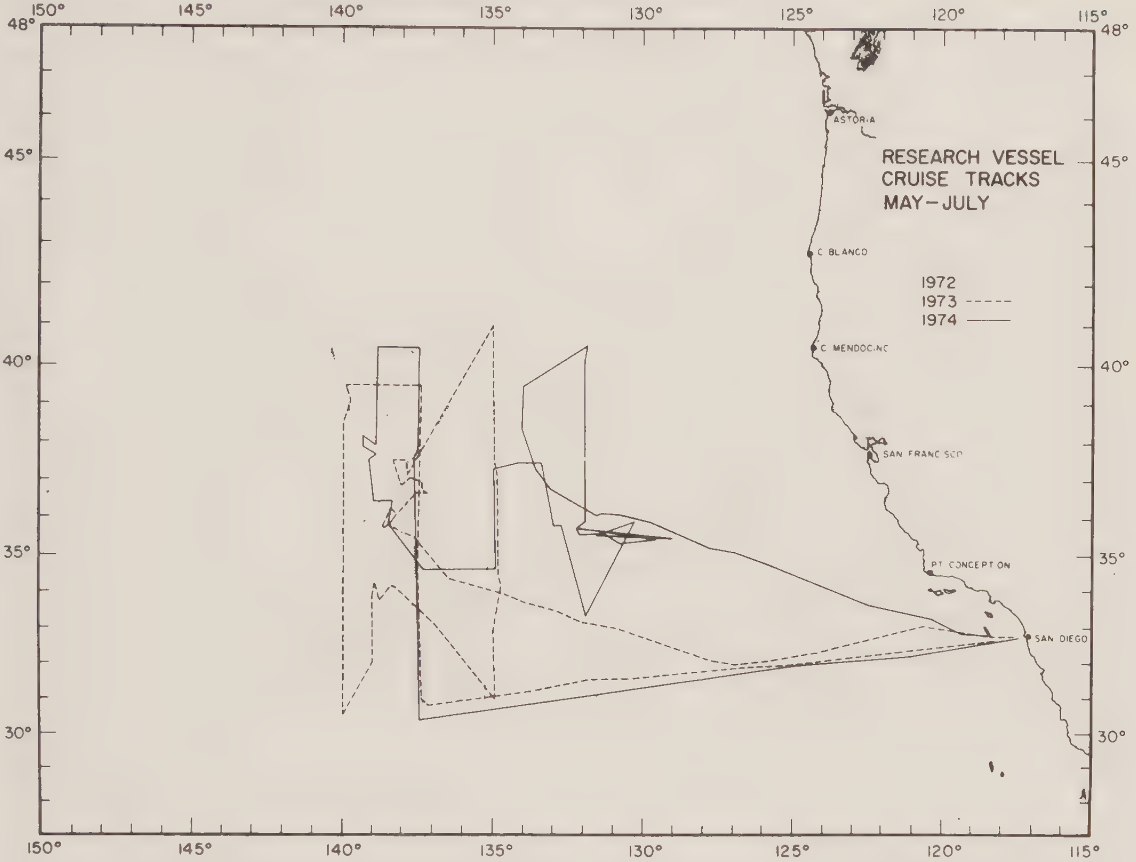

FIGURE 1.—Albacore research vessel cruise tracks for the 1972-74 offshore research surveys.

oblique midwater trawl hauls using an Isaacs-Kidd Midwater Trawl. Also, surface temperature, salinity, and chlorophyll were recorded continuously while underway.

Generally, 10 jiglines (five on *Townsend Cromwell* cruise in 1972) were trolled for albacore on transects between oceanographic stations during daylight. In some regions that were not covered by fishing vessels, trolling was carried on by the research vessel exclusively throughout daylight. On such fishing days, three or four expendable bathythermograph (XBT) drops were made in addition to continuous monitoring of surface temperature, salinity, and chlorophyll.

Operations Aboard Fishing Vessels

The AFRF charter vessels which took part in the offshore surveys were jigboats, except for two baitboats in 1973 which were outfitted to conduct either live-bait fishing or jig fishing. Twelve fishing vessels participated in the operations in 1972 and 1973 and five in 1974.

The fishing vessels sailed in groups of four from San Diego, Calif., and Astoria, Oreg., at 15- to 20-day intervals during 1972 and 1973, and all vessels sailed together from San Diego in 1974. The vessels usually worked in pairs. A schematic diagram of the cruise tracks for the 1972-74 offshore surveys is shown in Figure 3. Detailed cruise tracks showing daily positions and locations of XBT stations for each fishing vessel or pair of fishing vessels by 10-day period are given in Lynn and Laurs[7] (see footnotes 3 and 4).

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[7] Lynn, R. J., and R. M. Laurs. 1974. Cooperative NMFS-AFRF early season offshore studies conducted during 1974. *In* Report of joint National Marine Fisheries Service-American Fishermen's Research Foundation albacore studies conducted during 1974, p. 3-18. Southwest Fish. Cent. Admin. Rep. LJ-74-47.

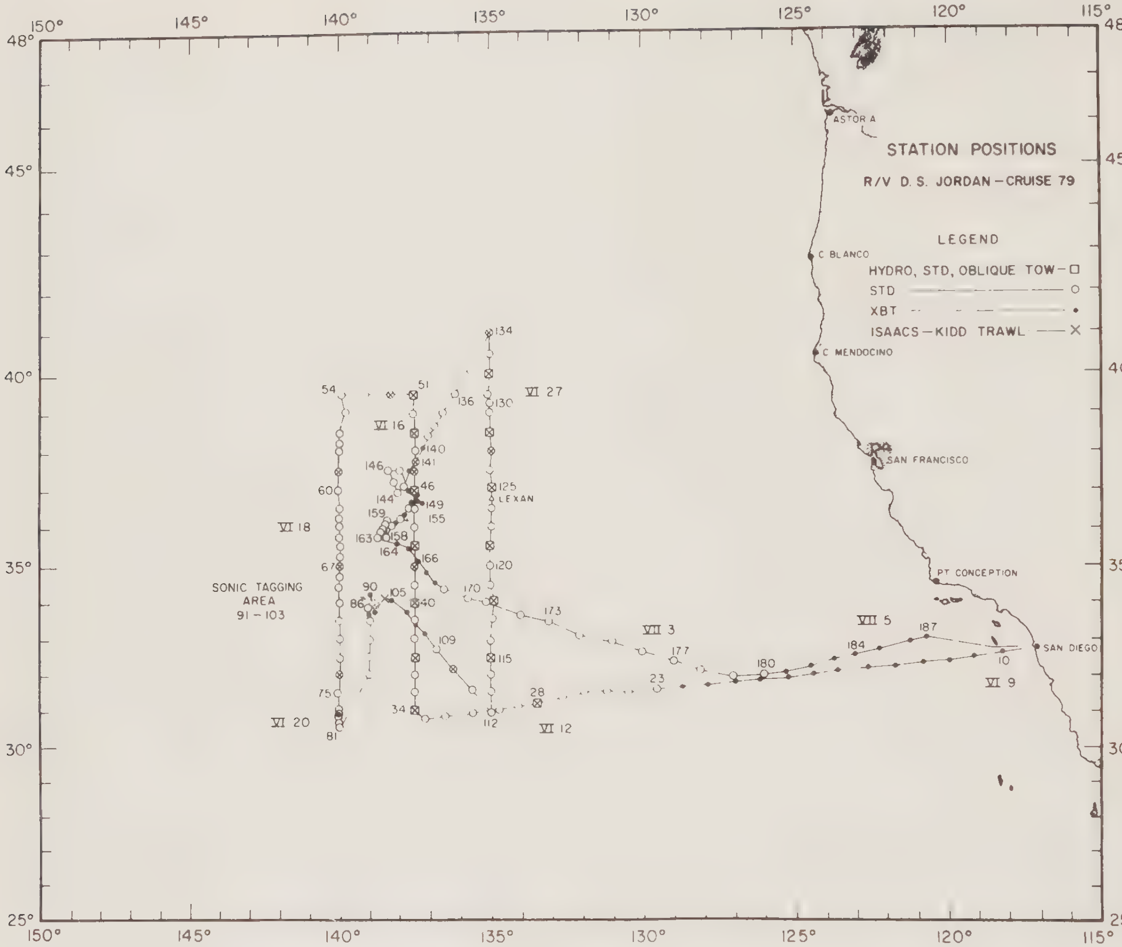

STATION POSITIONS
R/V D. S. JORDAN – CRUISE 79
LEGEND
HYDRO, STD, OBLIQUE TOW – □
STD – ○
XBT – •
ISAACS – KIDD TRAWL – X
ASTORIA
C BLANCO
C MENDOCINO
SAN FRANCISCO
PT CONCEPTION
SAN DIEGO
SONIC TAGGING AREA 91 – 103
LEXAN
VI 16
VI 18
VI 20
VI 27
VI 12
VII 3
VII 5
VI 9
54
51
136
130
134
140
141
146
46
125
144
149
155
60
159
163
158
164
166
67
120
90
105
86
40
170
173
177
109
115
23
180
184
187
10
28
75
34
112
81
150°
145°
140°
135°
130°
125°
120°
115°
48°
45°
40°
35°
30°
25°

FIGURE 2.—Track and station positions for RV *David Starr Jordan* cruise 79, 9 June-6 July 1973.

Standard commercial albacore fishing equipment and regular commercial fishing methods were used. Most of the jig vessels trolled 10 lines and baitboats 6 or 8 lines when jig fishing. (Baitboats had better success when trolling than when baitfishing.) Daily records pertaining to fishing operations were maintained aboard each vessel, including number of fish caught, fork length of most fish caught (except for two vessels in 1972), positions where fishing was started and ended, amount of fishing effort expended, and fishing conditions and signs of fish. In addition, sea-surface temperature, sea conditions, and surface weather conditions were recorded. Half of the fishing vessels chartered in 1972 and 1973, and all in 1974, were equipped with an XBT system; generally one or two XBT probes were launched each day. Sea-surface temperature measurements were made using bucket thermometers.

EARLY SEASON DISTRIBUTION AND RELATIVE ABUNDANCE OF ALBACORE IN OFFSHORE WATERS

Distribution of Catches Made By Charter Vessels

Nearly 27,000 albacore were caught by the chartered fishing vessels during the three offshore surveys (Table 1). In all three surveys, albacore were taken in substantial numbers in an offshore region between lat. 31° and 36°N from late May through June. Catch rates were generally low or zero in surrounding regions and during explorato-

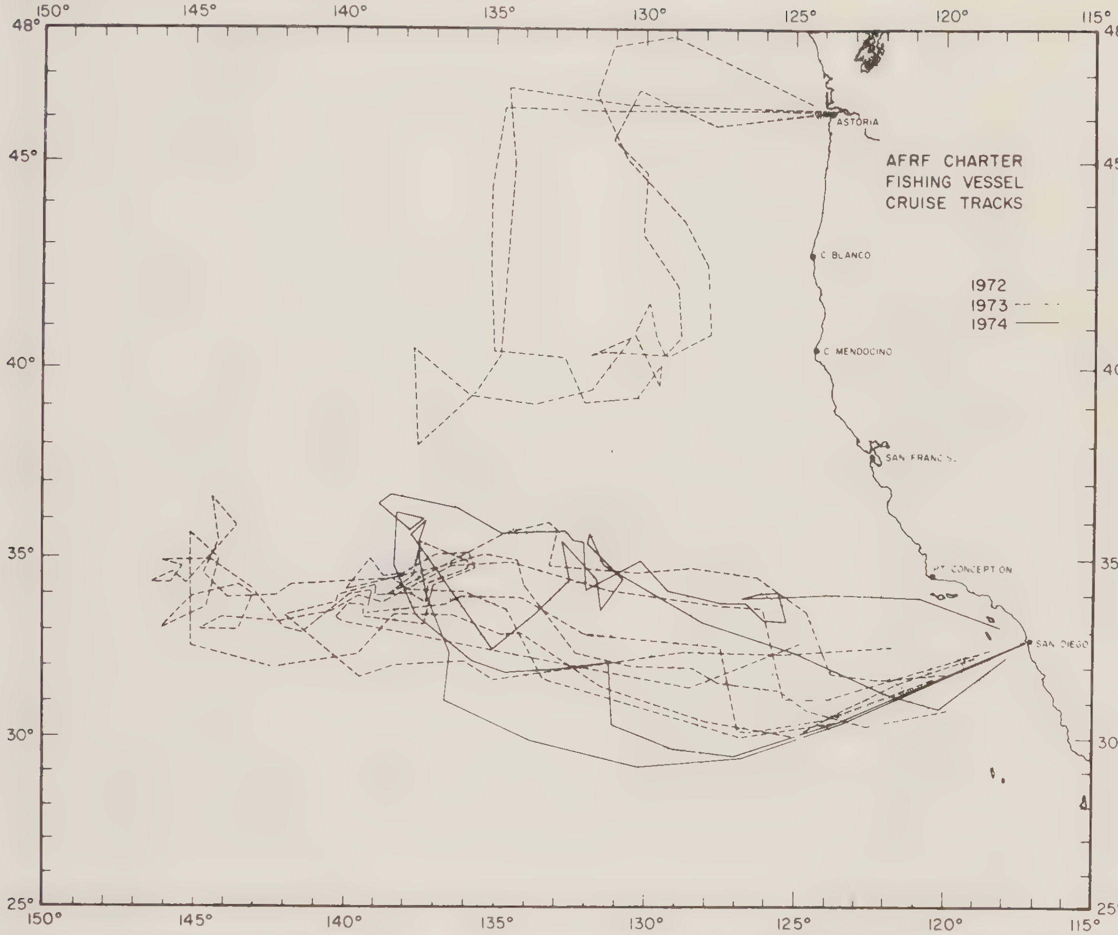

150°
145°
140°
135°
130°
125°
120°
115°
48°
45°
40°
35°
30°
25°
ASTORIA
AFRF CHARTER
FISHING VESSEL
CRUISE TRACKS
C BLANCO
C MENDOCINO
1972
1973
1974
SAN FRANCISCO
PT CONCEPTION
SAN DIEGO

FIGURE 3.—American Fishermen's Research Foundation charter fishing vessel cruise tracks for the 1972-74 offshore research surveys.

ry fishing before late May. Variations in distribution and relative abundance of albacore were observed within and between surveys.

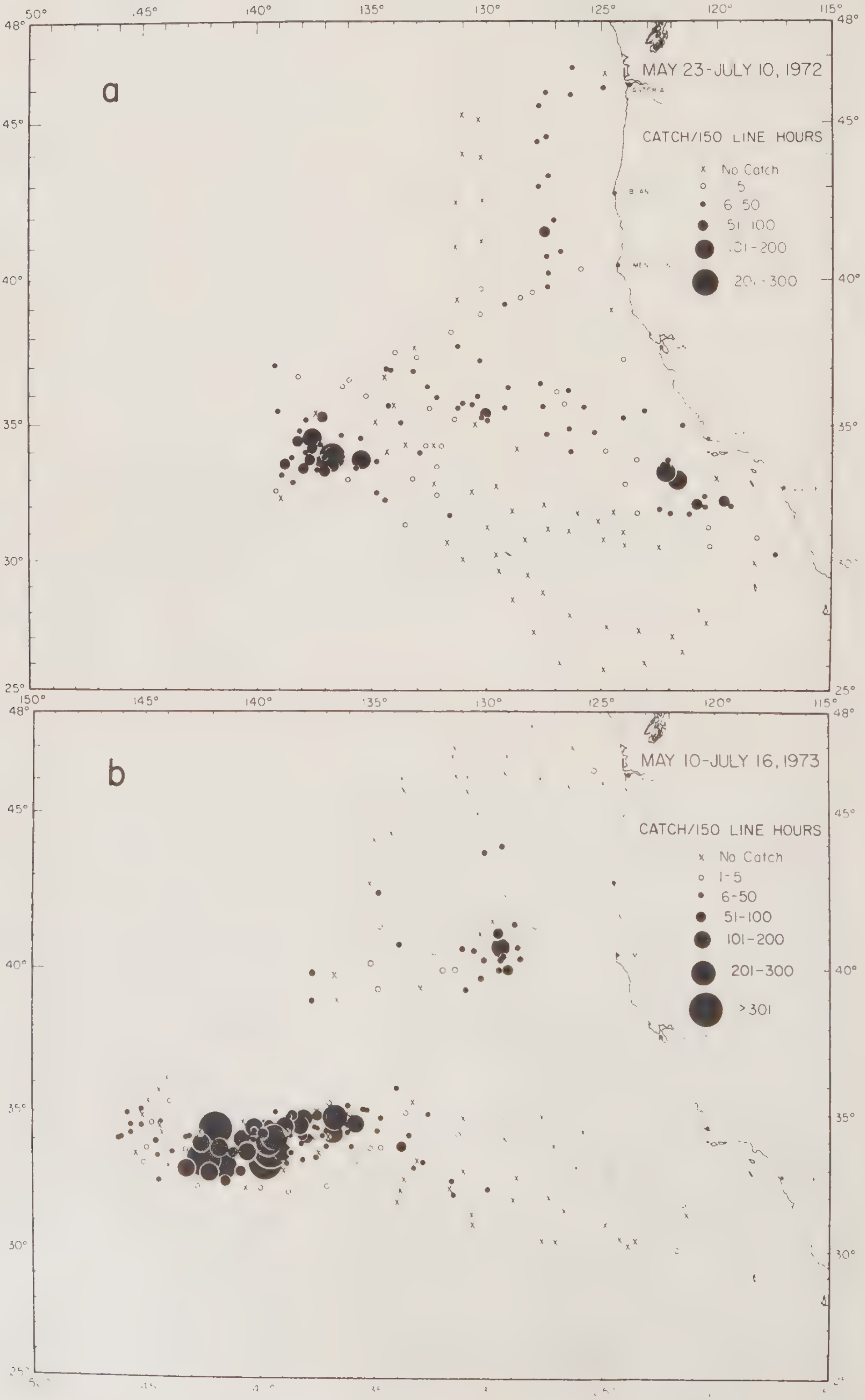
Differences Between Surveys

Plots of the charter vessel catches for each survey are given in Figures 4a-c. The catches represented in these and other plots have been standardized to the number of fish caught per 150 line-hours (averaged between pairs of vessels that fished together for 1972 and 1973) and presented graphically by proportionately increasing size of dots.

TABLE 1.—Albacore survey catches.

Year	Total catch by charter vessels	Tagged and released	Total catch by research vessel
1972	6,746	1,431	155
1973	11,027	1,738	130
1974	9,146	1,369	495
Total	26,919	4,538	780

In 1972 and 1973, relative abundance of albacore was high between lat. 32° and 35°N, long. 135° and 140°W, and lat. 32° and 35°N, long. 135° and 143°W, respectively (Figure 4a-b). In both of these years small or no catches were made in the region between long. 135°W and inshore waters within 150 mi of the coast where fishing takes place during the traditional albacore fishing season. In 1974 (Figure 4c), high catch rates were again made offshore of long. 135°W, but over a larger latitudinal range, lat. 31° to 36°N, and somewhat more scattered than in the two preceding years. Also, high catches were made at about lat. 33° to 36°N, long. 124° to 135°W in the region between


a
MAY 23-JULY 10, 1972
CATCH/150 LINE HOURS
x No Catch
○ 1-5
• 6-50
● 51-100
● 101-200
● 201-300
ASTORIA
150°
145°
140°
135°
130°
125°
120°
115°
48°
45°
40°
35°
30°
25°
b
MAY 10-JULY 16, 1973
CATCH/150 LINE HOURS
x No Catch
○ 1-5
• 6-50
● 51-100
● 101-200
● 201-300
● >301

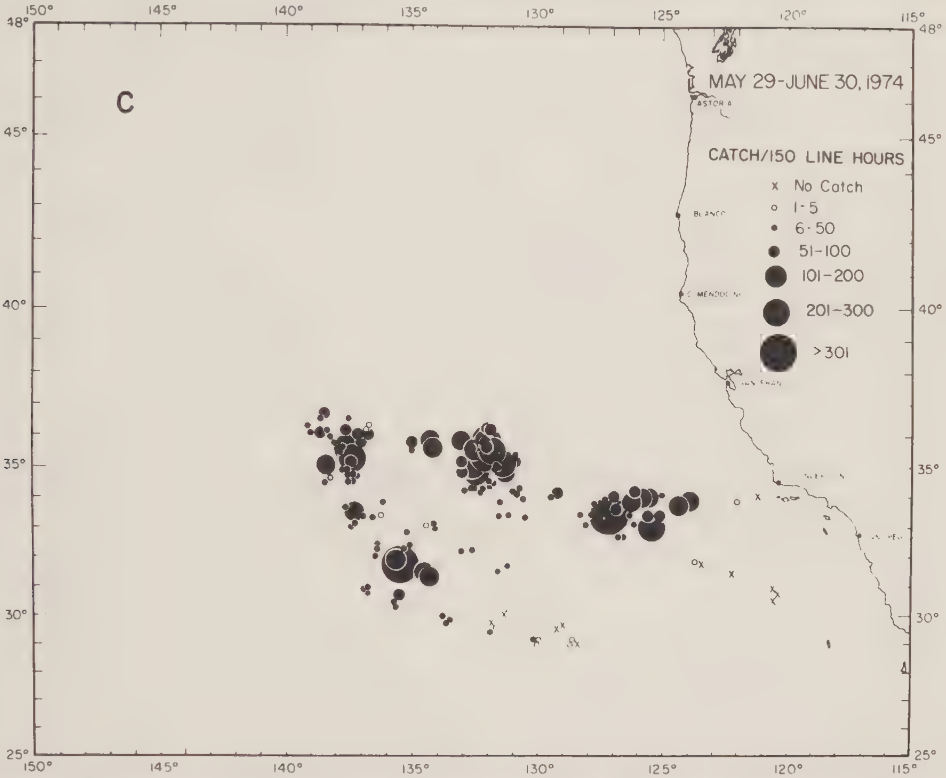
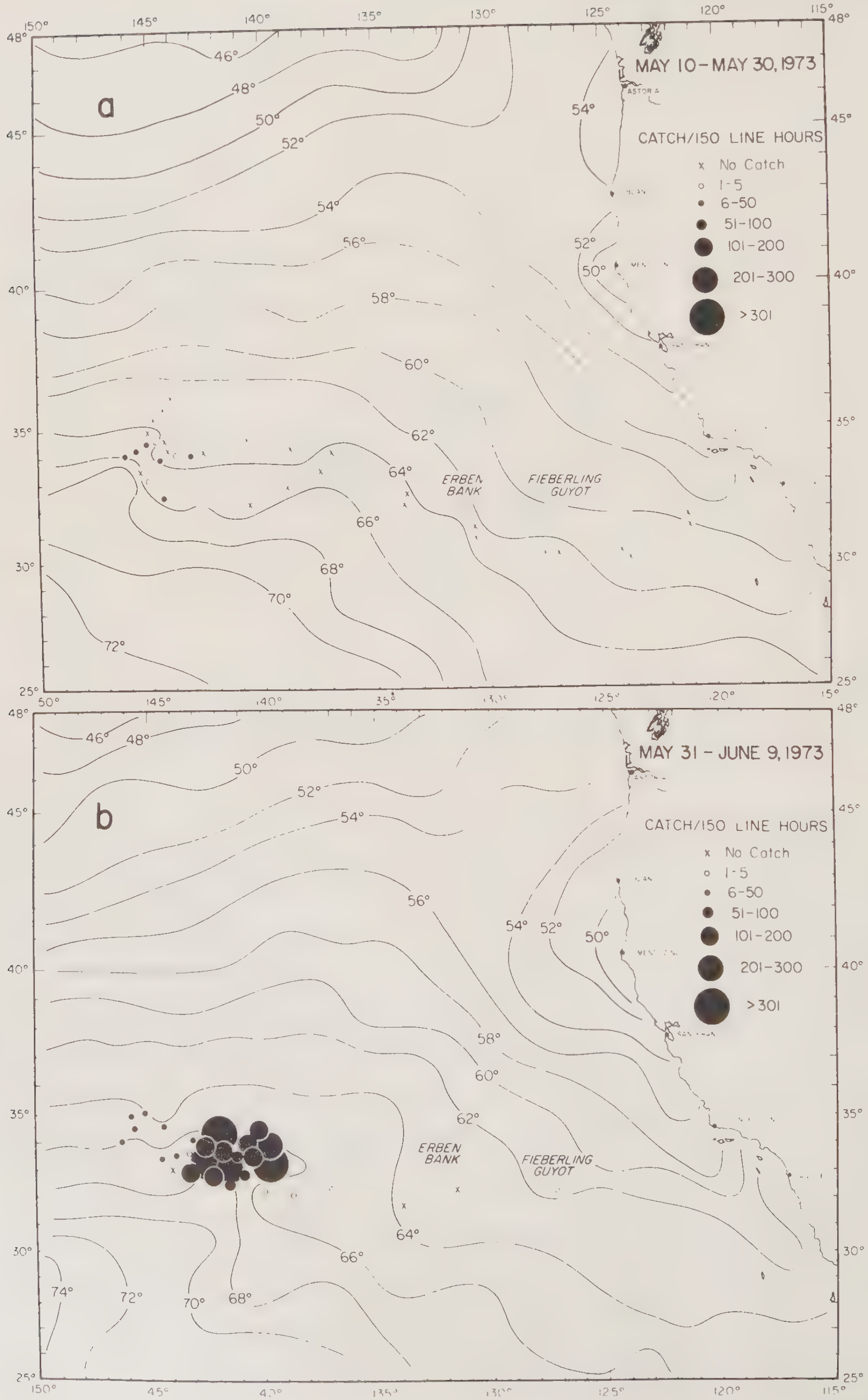


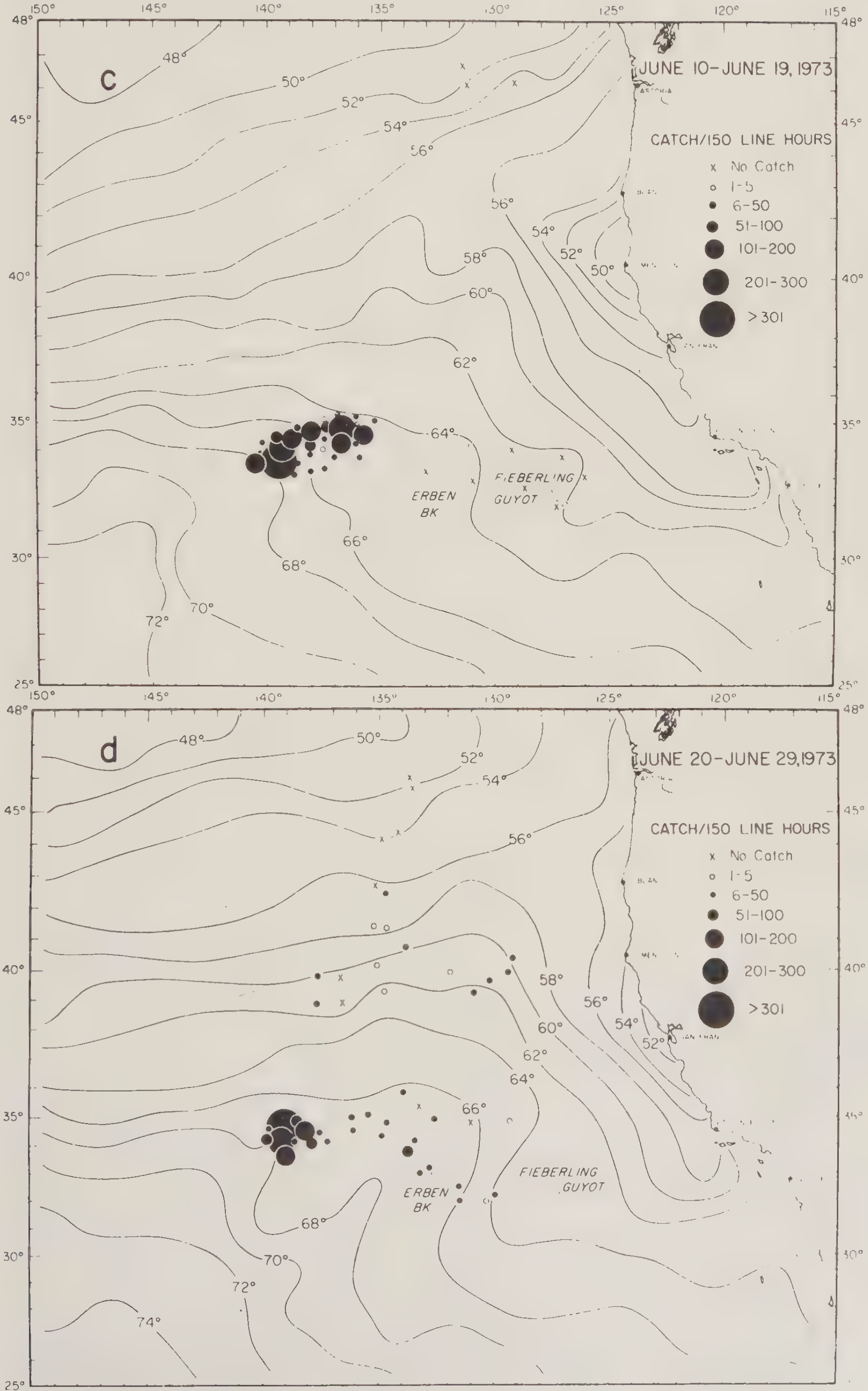
FIGURE 4.—Albacore catch per 150 line-hours by American Fishermen's Research Foundation charter vessels: a. 23 May-10 July 1972; b. 10 May-16 July 1973; c. 29 May-30 June 1974.

the offshore area of high catches and inshore waters.

Differences Within Surveys

Representative information on spatial and temporal variations in the distribution and relative abundance of albacore in offshore waters during May and June is given in Figure 5a-e. In the early part of the 1973 survey, 10 to 30 May, four vessels worked westward making only small scattered catches between lat. 31° and 35°N, long. 142° and 145°W. In the second time period, 31 May to 9 June, the vessels returned through waters they had scouted earlier and began making catches of over 100 fish/day between lat. 32° and 34°N, long. 139° and 143°W. Good catches continued to be made in the general area of lat. 33° to 35°N, long. 135° to 143°W for several weeks with charter vessels landing up to 300 fish/day on many days. A second group of four charter boats, which left San Diego on 25 May, did not catch any fish until 4 June when they moved westward of long. 139°W near lat. 33° to 35°N. On their return to San Diego during mid-June, the first group of boats failed to catch any fish east of long. 135°W despite favorable ocean temperature conditions. Similarly, on the return to San Diego near the end of June, catches by the second group of charter boats dropped off abruptly east of long. 135°W with only small scattered or no catches made east of Fieberling Guyot (long. 128°W). The four vessels surveying the area north of lat. 38°N found generally poor to moderate catches. (The region lat. 35° to 38°N was not covered by the fishing vessels.) This sequence of catch charts shows that: 1) albacore were apparently unavailable to jig fishing, except for scattered catches, through May in a region which subsequently was to prove very productive; 2) albacore became available to trolling gear in the first week of June in a region which will be shown later to be associated with the subtropic boundary of the Transition Zone; 3) good catches persisted within a block of 2° latitude by 7° longitude for


a
MAY 10 – MAY 30, 1973
CATCH/150 LINE HOURS
x No Catch
○ 1-5
● 6-50
● 51-100
● 101-200
● 201-300
● >301
ASTORIA
46°
48°
50°
52°
54°
56°
58°
60°
62°
64°
66°
68°
70°
72°
ERBEN BANK
FIEBERLING GUYOT
b
MAY 31 – JUNE 9, 1973
74°
150°
145°
140°
135°
130°
125°
120°
115°
48°
45°
40°
35°
30°
25°


c
JUNE 10–JUNE 19, 1973
CATCH/150 LINE HOURS
x No Catch
○ 1-5
● 6-50
● 51-100
● 101-200
● 201-300
● >301
ASTORIA
ERBEN BK
FIEBERLING GUYOT
48°
50°
52°
54°
56°
58°
60°
62°
64°
66°
68°
70°
72°
150°
145°
140°
135°
130°
125°
120°
115°
45°
40°
35°
30°
25°
d
JUNE 20–JUNE 29, 1973
CATCH/150 LINE HOURS
x No Catch
○ 1-5
● 6-50
● 51-100
● 101-200
● 201-300
● >301
ERBEN BK
FIEBERLING GUYOT
74°

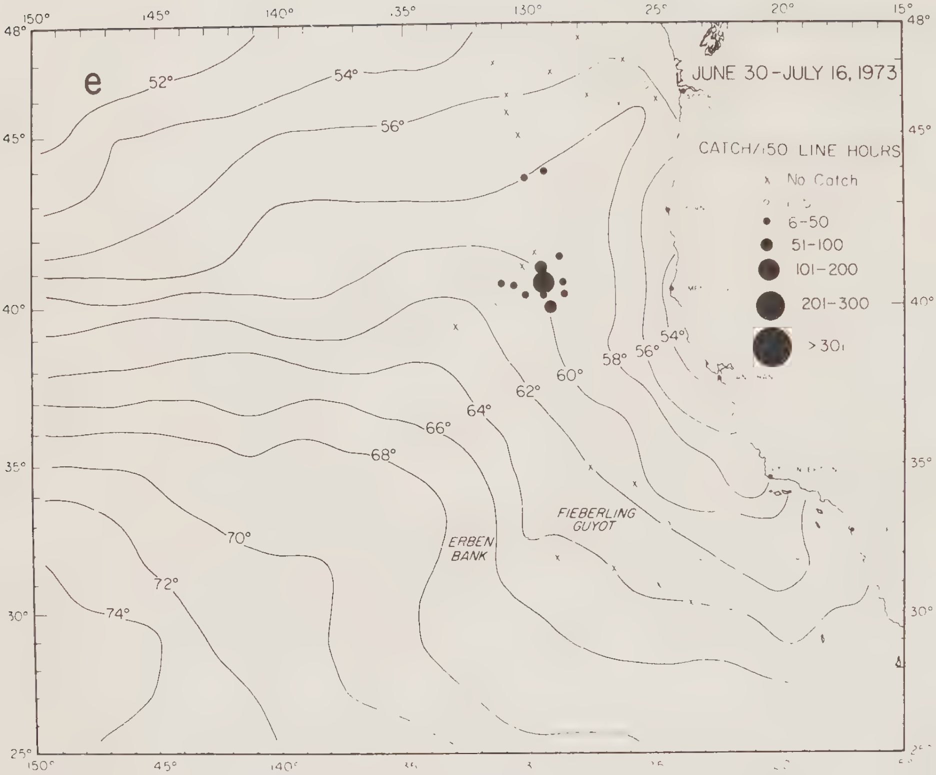


FIGURE 5.—Albacore catch per 150 line-hours by American Fishermen's Research Foundation charter vessels and sea-surface temperature: a. 10-30 May 1973; b. 31 May-9 June 1973; c. 10-19 June 1973; d. 20-29 June 1973; e. 30 June-16 July 1973.

over a 3-wk period in June, and 4) elsewhere catches were substantially lower.

Catches Made By Noncharter Commercial Fishing Vessels

Because of the fishing success of the chartered fishing vessels, in the years following the first survey (1972), noncharter commercial albacore vessels have fished in the offshore region concurrently with the chartered fishing vessels and research vessels. During June 1973 and June 1974 it is estimated that, respectively, 25 to 30 and 50 to 60 albacore vessels fished across a large zone of latitudes in the offshore regions (Jack Bowland pers. commun.). Additional information on the distribution and relative abundance of albacore is provided by these catch data.

Figure 6a-e shows estimates of mean catch-per-unit effort by 15-day period and 1° quadrangle of latitude and longitude for May through July 1973, for those commercial albacore vessels from which logbook records were available. [Logbook records were standardized by methods given in Laurs et al. (1976).]

As with the charter vessels, a center of high relative abundance was found in the offshore region between lat. 33° and 35°N and long. 139° and 143°W. From mid-May through mid-June (Figure 6a, b) no catches were reported north of lat. 36°N nor (with one exception) east of long. 134°W. In the latter half of June (Figure 6c), a scattering of catches was made in the intervening zone. The distribution and relative abundance of albacore, indicated by the charter and noncharter fishing vessel catches, were similar. Catches by noncharter vessels were made over the same latitudinal range and the same offshore to nearshore sequence was observed. The fishing success of the noncharter vessels further demonstrates that commercial concentrations of albacore were available 4 to 6 wk earlier than the normal fishing season in waters hundreds of miles offshore of the area where the fishery has traditionally operated.

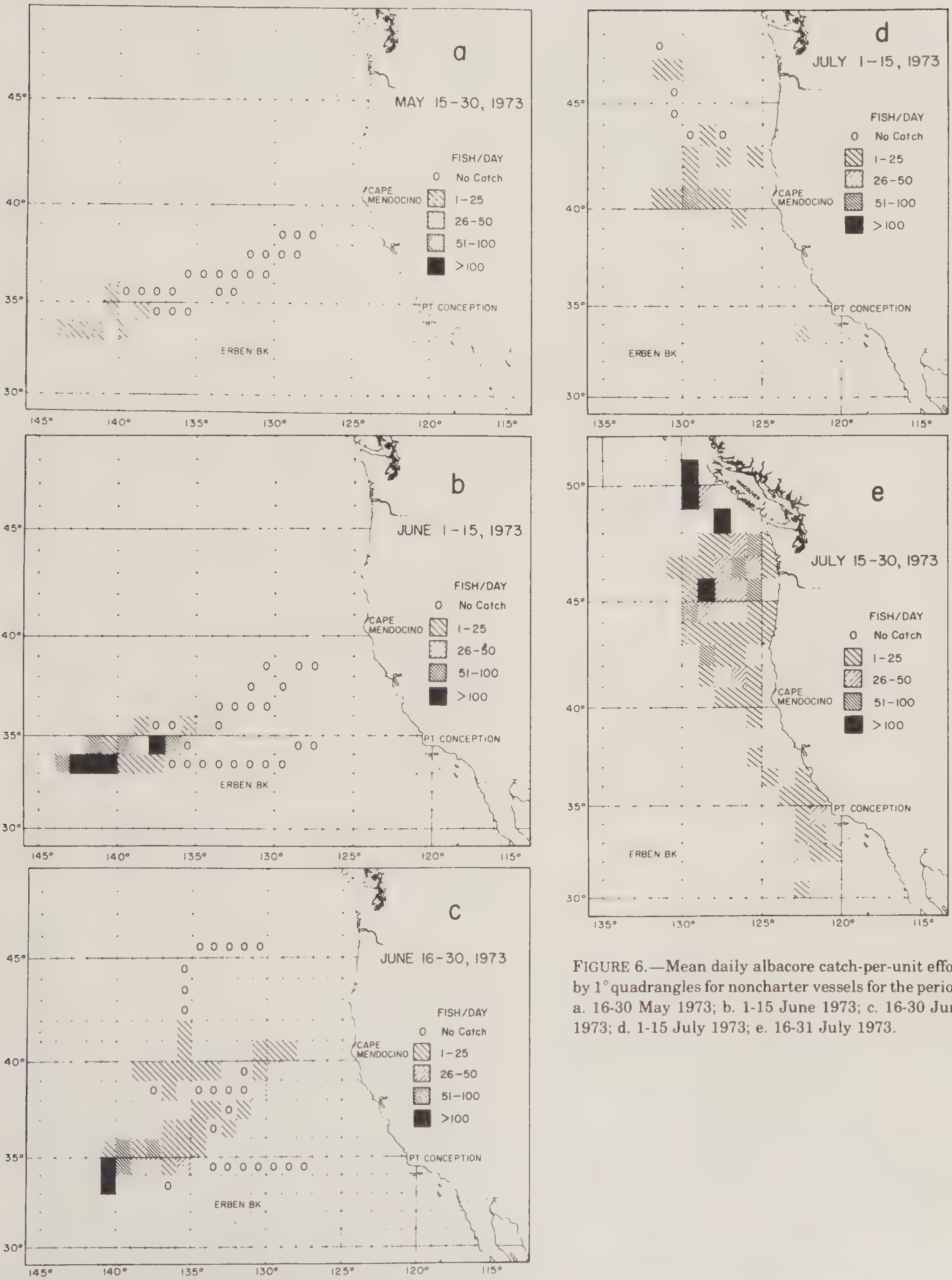

a
MAY 15-30, 1973
b
JUNE 1-15, 1973
c
JUNE 16-30, 1973
d
JULY 1-15, 1973
e
JULY 15-30, 1973
FISH/DAY
0 No Catch
1-25
26-50
51-100
>100
CAPE MENDOCINO
PT CONCEPTION
ERBEN BK
30°
35°
40°
45°
50°
145°
140°
135°
130°
125°
120°
115°

FIGURE 6.—Mean daily albacore catch-per-unit effort by 1° quadrangles for noncharter vessels for the period: a. 16-30 May 1973; b. 1-15 June 1973; c. 16-30 June 1973; d. 1-15 July 1973; e. 16-31 July 1973.

The last two charts in this series (Figure 6d, e, through the end of July 1973) reveal subsequent stages of albacore migration and commencement of the nearshore fishery. The relative abundance of albacore was high in nearshore waters by late July. In comparison to recent years, the 1973 nearshore fishery started about 3 weeks late.

SIZE COMPOSITION OF FISH

Three size modal groups of fish were caught in each year by the AFRF charter vessels; however, the relative proportions of the size groups varied among the years (Figure 7; Table 2). In 1972 about equal proportions of each size modal group were caught. In 1973 and 1974 the medium-size modal group was predominant and the larger one nearly absent.

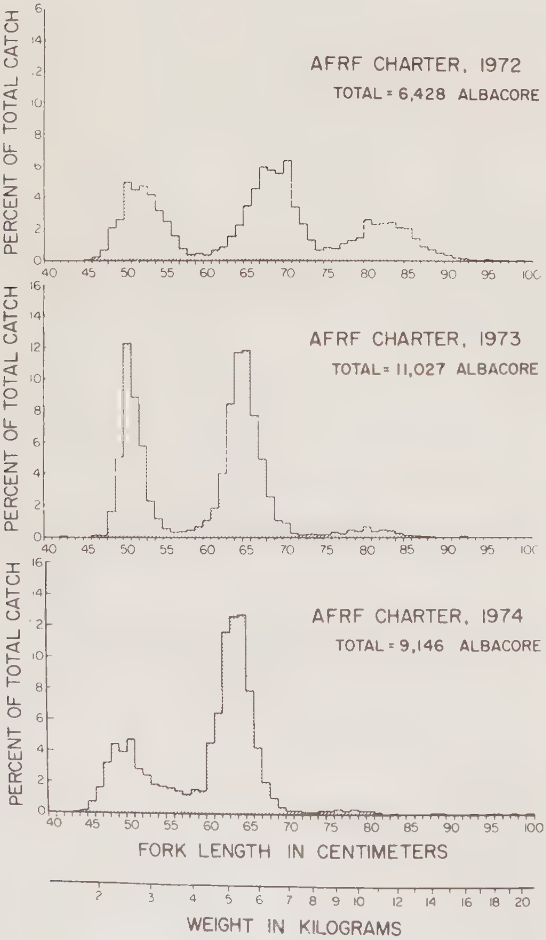


FIGURE 7.—Size composition by percent frequency of catch versus fork length for total catches of albacore from the research surveys in 1972-74.

TABLE 2.—Percentage size composition by number and by weight for albacore catches made by American Fishermen's Research Foundation charter vessels in the offshore area west of long. 130°W and south of lat. 38°N.

Year	<4 kg	4-8 kg	>8 kg	<4 kg	4-8 kg	>8 kg
		Percent by number			*Percent by weight*[1]	
1972	39	33	27	18	33	49
1973	43	53	4	25	65	10
1974	37	61	2	22	73	5

[1] Estimated from length-weight relationship given by Clemens (1961).

THE MARINE ENVIRONMENT

Albacore were found mainly in Transition Zone waters. Variations in distribution and relative abundance between each of the surveys appeared to be related to oceanographic conditions of the Transition Zone. Transition Zone waters lie between the cool low salinity Pacific Subarctic waters to the north and the warm, saline Eastern North Pacific Central waters to the south and have temperatures and salinities that are characteristic of a mixture of these two primary water masses (Sverdrup et al. 1942; Christensen and Lee 1965). Transition Zone waters are found in a band across the North Pacific middle latitudes within the North Pacific Current and are bounded by sharp horizontal gradients in temperature and salinity (McGary and Stroup 1956; Roden 1970, 1972, 1975). These bounding gradient regions are sometimes referred to as the Subtropic and Subarctic fronts. The dynamic processes which produce and maintain these gradients also enrich these waters (McGary and Stroup 1956).

An oceanographic section of the vertical distribution of temperature and salinity was taken along long. 137°30′W in June 1972, 1973, and 1974 (Figure 8). In 1972 and 1973, Subarctic waters were found north of lat. 35 °N and Central waters south of lat. 31°30′N and 32°N, respectively. Boundaries of the Transition Zone between these water masses were well developed and readily identifiable. The Subarctic front was marked by abrupt shoaling of the 33.8‰ isohaline and 58°F (14.4°C) isotherm and a sharp horizontal gradient in salinity extending from the surface to greater than 175 m. The Subtropic front was delineated by steep shoaling of the 34.2‰ isohaline and 62°F (16.7°C) isotherm and a sharp gradient in salinity extending from the surface to greater

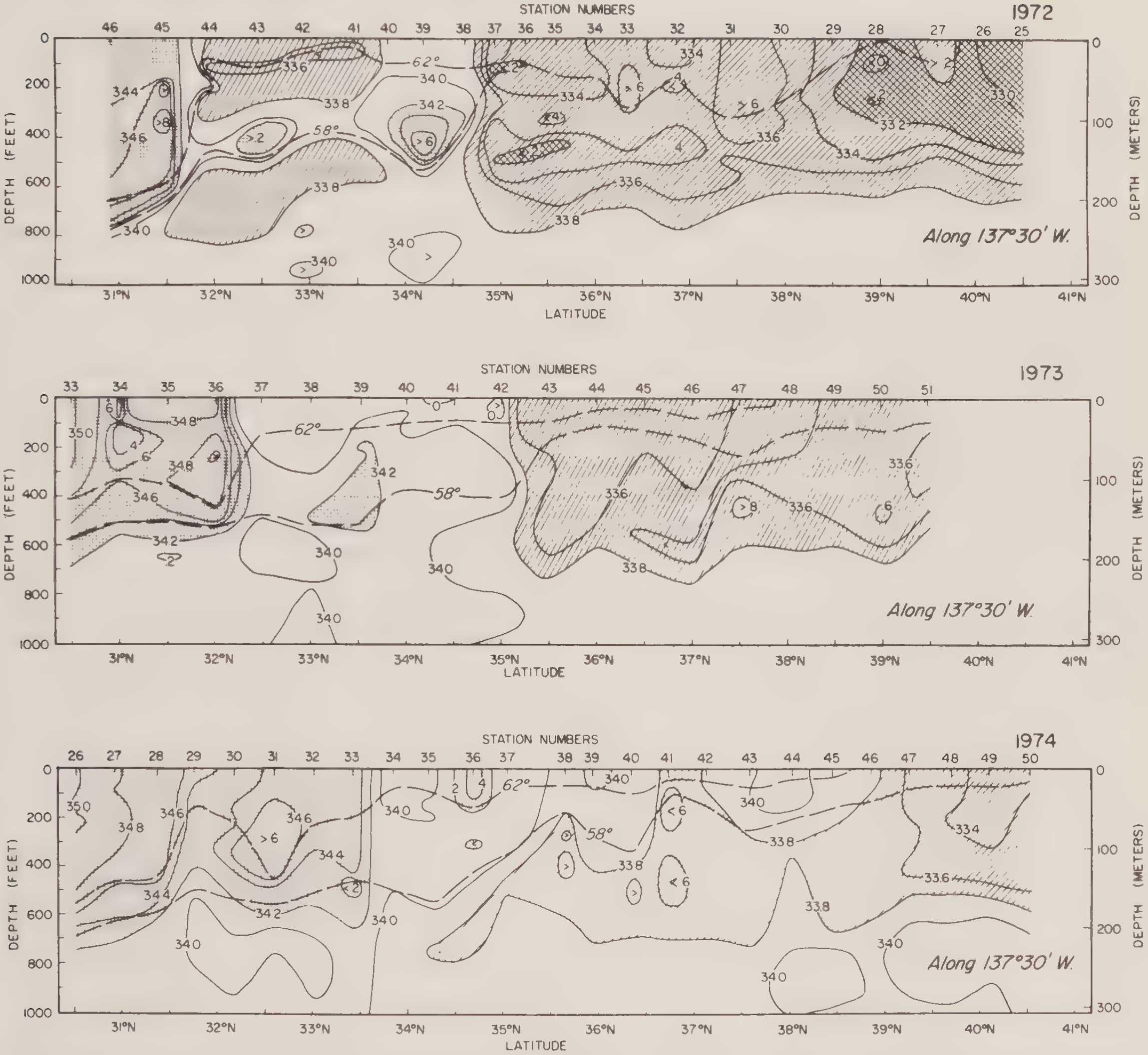


FIGURE 8.—Vertical sections of temperature and salinity along long. 137°30′W during June 1972, 1973, and 1974. Low salinity water (<33.8‰) indicative of Subarctic water is hatched and crosshatched. High salinity water (>34.2‰) indicative of Central water is shaded with a dot pattern. The 58° and 62 F isotherms are shown by heavy dashed lines.

than 150 m. A temperature gradient on the order of 0.6°C in 13 km was often found to mark these fronts at the sea surface. At other times, however, seasonal heating in the surface layer eroded the horizontal temperature gradient at the surface. Mixing was evident in the Transition Zone in 1972 with low-salinity water penetrating southward and some high-salinity water northward at intermediate depths.

Oceanographic conditions were different in the region of the Transition Zone in 1974 from those which were observed in 1972 and 1973. In 1974, boundaries of the Transition Zone were poorly developed and broken. Salinity gradients were diffuse and changes in depth of the isotherms gradual and variable in the regions of the Subarctic and Subtropic fronts. The Subarctic front was virtually nonexistent and Transition Zone waters graded gradually into Subarctic waters. The Subtropic front was weak and spread between lat. 31°30′ and 33°30′N. Saur[8] found that the diffuse nature of the Transition Zone and its frontal boundaries became evident late in 1973 and persisted throughout 1974.

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[8] Saur, J. F. T. 1976. Anomalies of surface salinity and temperature on the Honolulu-San Francisco route, June 1966-June 1975. NORPAX Highlights 4:2-4. (Unpubl. rep.)

ALBACORE CATCHES IN RELATION TO OCEANIC FRONTS

Graphical depictions of the frontal gradients that form the boundaries of the Transition Zone[9] and standardized albacore catches for June of each of the three surveys are shown in Figure 9a-c. This figure indicates that the catches were largely made within the Transition Zone in all 3 yr. During June 1972 and 1973, productive centers of fishing, indicating high relative abundance of albacore, developed in the Transition Zone between lat. 33° and 35°N and west of long. 135°W (Figure 9a, b). These centers persisted for several weeks before fishing effort was ended. In these years, the frontal structure was strongly developed and the Transition Zone easily identifiable. During June 1974 when the frontal structure was poorly developed and water mass boundaries were less distinct, catches were distributed over a larger range of latitude and longitude (Figure 9c). Overall catches in 1974 were substantial but they were not persistent in any area for more than a few days. Thus, while albacore were still associated with Transition Zone waters, the influence of extensive lateral mixing between water masses and the diffuse nature of the boundary frontal structure apparently failed to concentrate fish in a given location for periods of time as had apparently occurred in the previous 2 yr.

While graphical depictions of frontal structure outline the location of the boundaries associated with Transition Zone water (Figure 9a-c), they do not indicate the intensity of the gradients of the frontal structure. The frontal structure has been shown generally to have weak gradients during

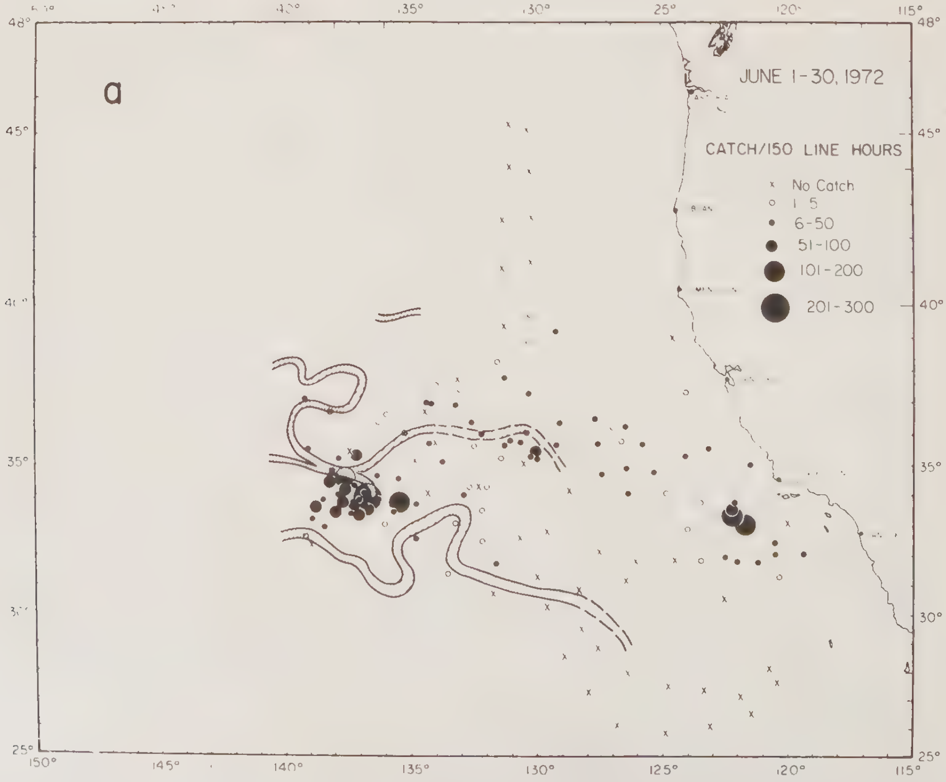

FIGURE 9.—Albacore catch per 150 line-hours by American Fishermen's Research Foundation charter vessels and locations of fronts delineating Transition Zone waters during: a. 1-30 June 1972; b. 1-30 June 1973; c. 1-30 June 1974.

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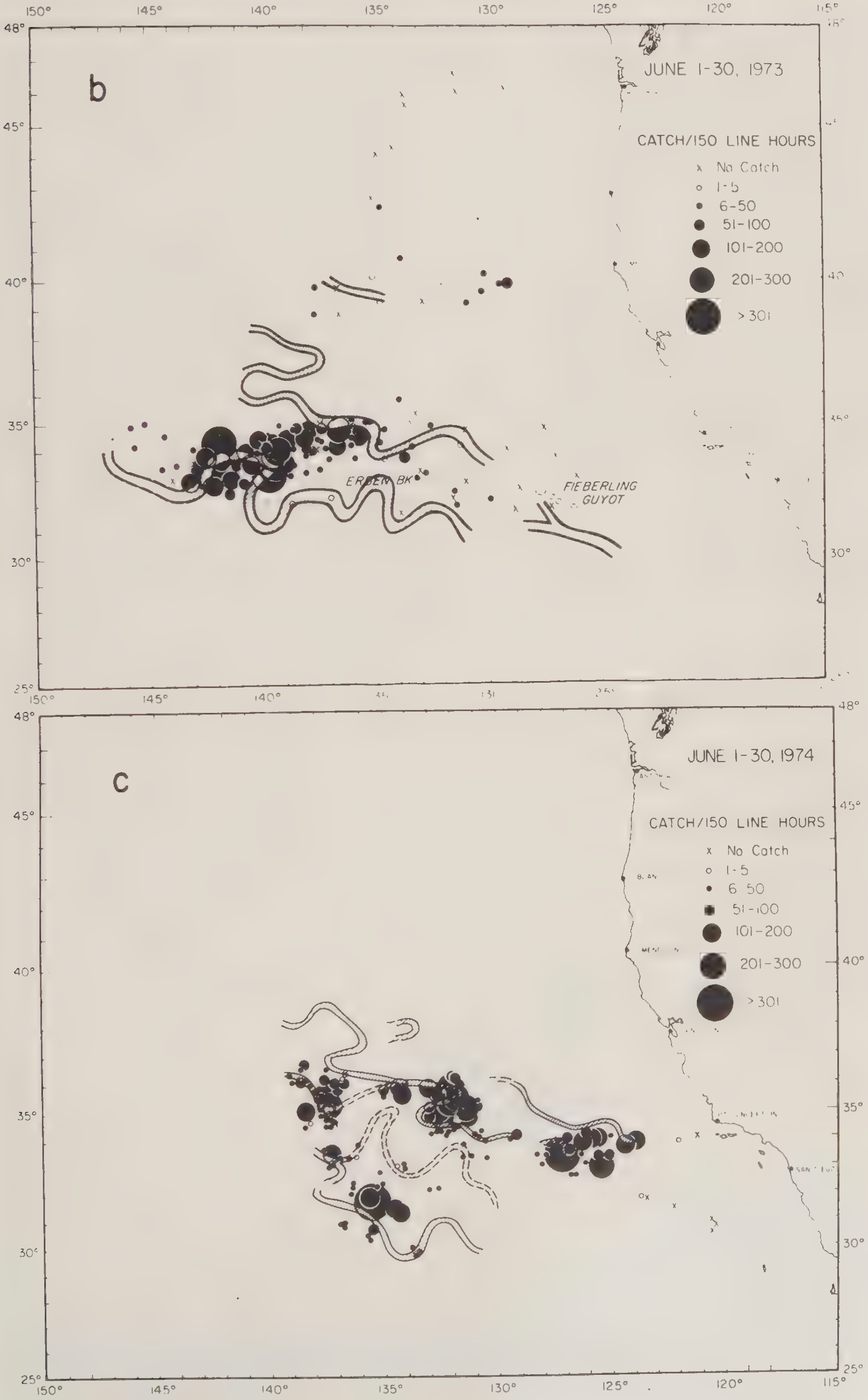
[9] The temperature and salinity fields measured by the research vessel, augmented by the XBT data collected by the charter fishing vessels, were analyzed to delineate the frontal gradients.


b
JUNE 1-30, 1973
CATCH/150 LINE HOURS
x No Catch
○ 1-5
● 6-50
● 51-100
● 101-200
● 201-300
● >301
ERBEN BK
FIEBERLING GUYOT
c
JUNE 1-30, 1974
CATCH/150 LINE HOURS
x No Catch
○ 1-5
● 6-50
● 51-100
● 101-200
● 201-300
● >301
150°
145°
140°
135°
130°
125°
120°
115°
48°
45°
40°
35°
30°
25°

June 1974; however, one localized area did have sharp, abrupt gradients. The eastward protruding tongue of Transition Zone water centered at lat. 35°30′N, long. 132°30°W had salinity gradients comparable with those found in previous years. Substantial catches of albacore persisted in this one region for a week after which fishing effort was terminated.

Further information on the distribution of albacore can be derived from the catches made by the research vessels (Figure 10a-c).[10] The research vessels trolled for albacore along tracks that crossed the oceanic fronts and expended fishing effort in Central, Subarctic, and Transition Zone waters. With few exceptions, they did not catch albacore in Central or Subarctic waters. In 1972 and again in 1973, when a large meander developed in the Subarctic front, albacore were taken in the northward protrusion of Transition Zone water (Figure 10a, b). Albacore often were found close to the front. During each of the surveys, catches were made by the research vessel as the frontal gradients were being recorded by shipboard instrumentation.

Analyses of variance were performed upon the charter vessel catch data to test the hypothesis that catch rates were dependent upon water mass in the offshore area during June. For the 1972 survey, daily or twice daily XBT casts were matched with the daily catch data. Because specific isotherms were found to fall within very different depth ranges from one water mass to another, the dependence of catch rate upon classes of depth ranges for these isotherms was tested. Thus for this statistical test the water masses may be defined as follows:

Water mass	*Isotherm*	*Depth*
Pacific Subarctic	58°F (14.4°C)	<60 m
Transition Zone	58°F	≥60 m

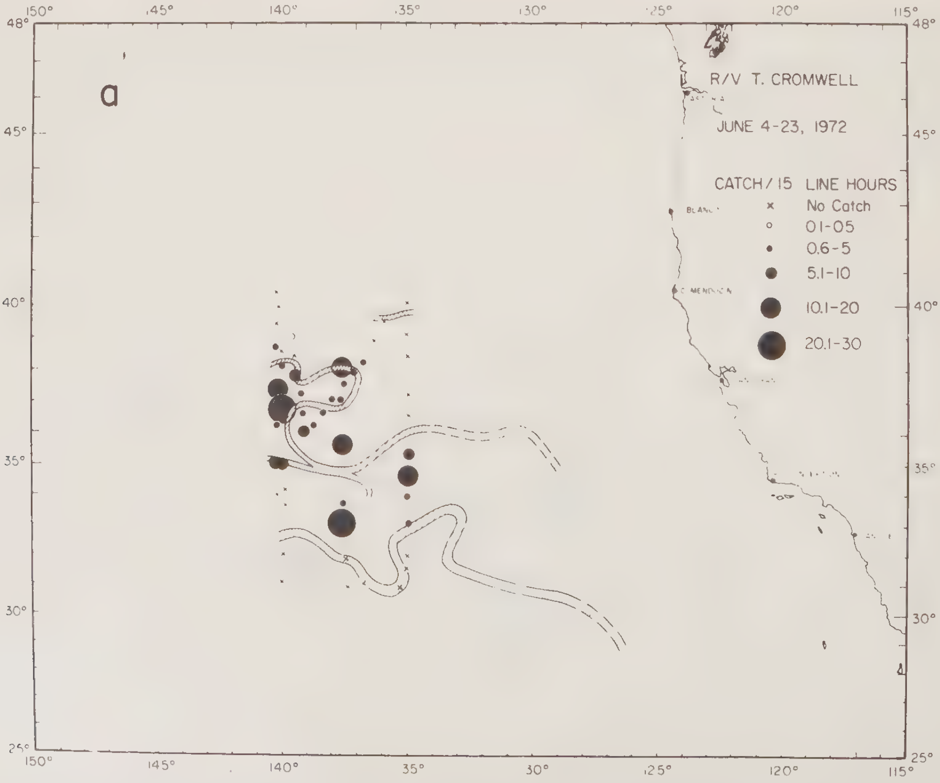


FIGURE 10.—Albacore catch per 15 line-hours by National Marine Fisheries Service research vessel and location of fronts delineating Transition Zone waters during: a. 4-23 June 1972; b. 9 June-5 July 1973; c. 29 May-1 July 1974.

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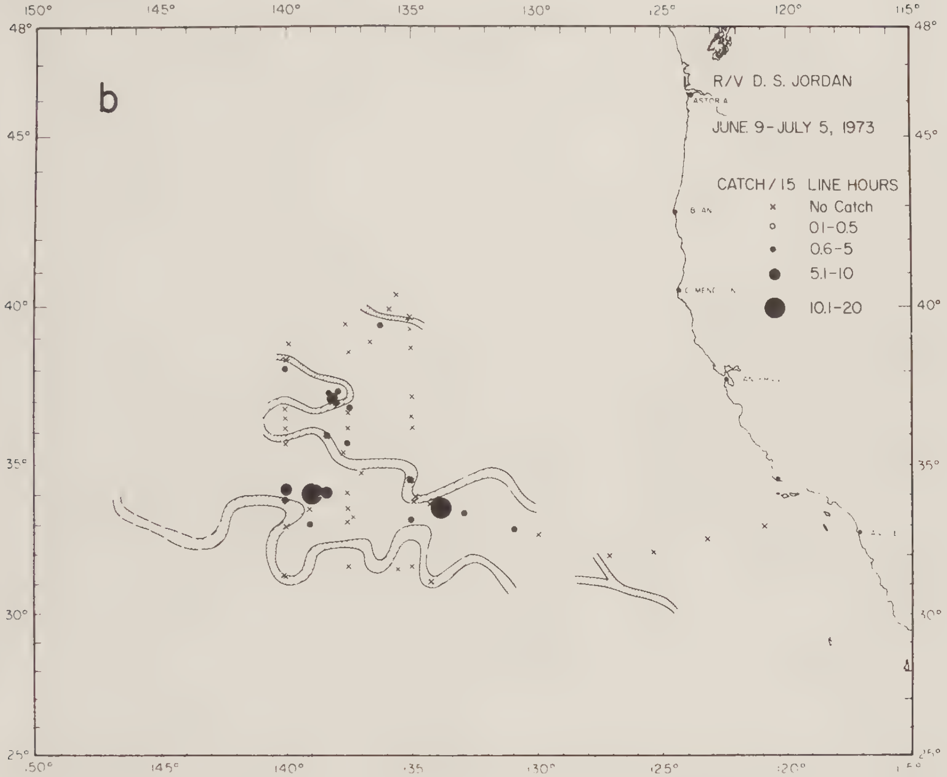
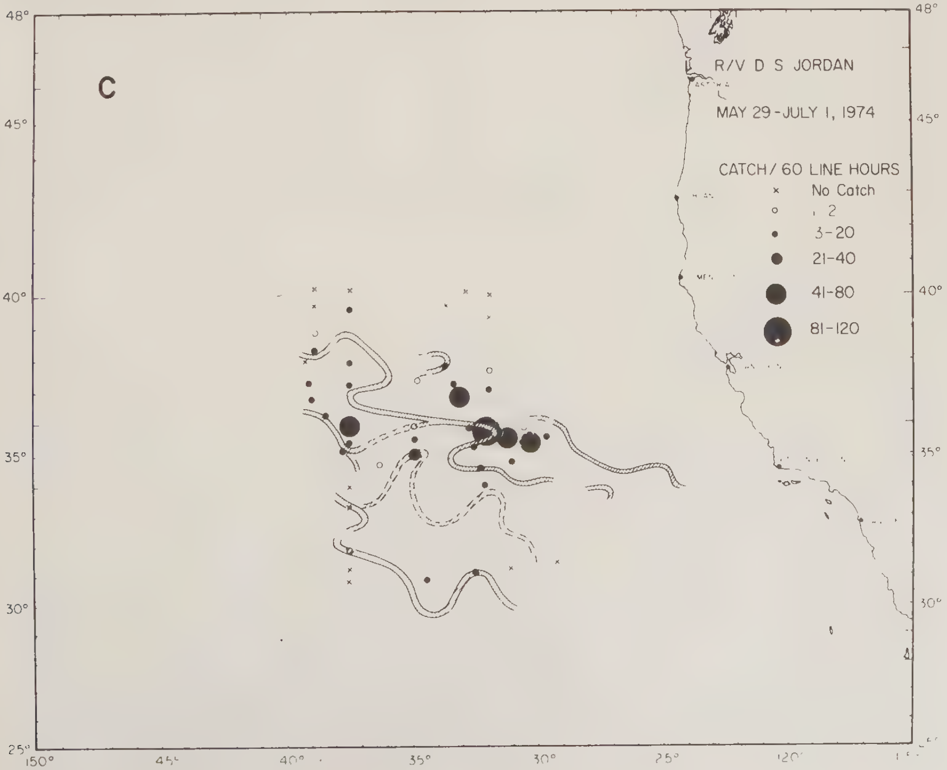
[10] Catches are expressed in number of fish caught per 15 line-hours in 1972 and 1973 and per 60 line-hours in 1974. These numbers of line-hours approximate the amount of fishing effort expended each day by the research vessels during respective years.


b
R/V D. S. JORDAN
JUNE 9-JULY 5, 1973
CATCH / 15 LINE HOURS
× No Catch
○ 0.1-0.5
• 0.6-5
● 5.1-10
● 10.1-20
150° 145° 140° 135° 130° 125° 120° 115°
48° 45° 40° 35° 30° 25°


c
R/V D S JORDAN
MAY 29-JULY 1, 1974
CATCH / 60 LINE HOURS
× No Catch
○ 1-2
• 3-20
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● 41-80
● 81-120
150° 145° 140° 135° 130° 125° 120° 115°
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	62°F (16.7°C)	≤90 m
Pacific Central	62°F	>90 m

The data were transformed to logarithms in order to standardize between-sample variance. Results of the analysis of variance show that mean catch in the Transition Zone, which was greatest, is significantly different ($P = 0.01$) from those in other water masses.

For the 1973 survey, both charter and noncharter vessel catches were available for test. The fronts were assumed fixed for this time frame, as shown in Figure 9b, and catches were assigned to a water mass based upon reported geographic position. Because no fishing effort was expended in Central waters, except close to the Subtropic front where catches are expected, an analysis of this division could not be included. Both the charter and noncharter vessel data revealed that mean catches were significantly greater ($P = 0.01$) in the Transition Zone than those in the Subarctic waters.

The poor development of the boundary fronts between water masses during 1974 precludes a definitive assignment of catch to water mass; therefore, a test of the 1974 data was not considered.

Catches made by both the charter fishing vessels and the research vessel during each of the three surveys demonstrate that albacore are distributed within the Transition Zone and may be absent (or unavailable) or nearly so in water masses to the north and south during this phase of their shoreward migration. Relative abundance is high in offshore areas within the Transition Zone waters and at times close to the oceanic fronts that form the boundaries of Transition Zone waters. Further, when the oceanic fronts are diffuse and widely spread there is likely to be a corresponding spread in the distribution of albacore and a dislocation of the centers of high relative abundance.

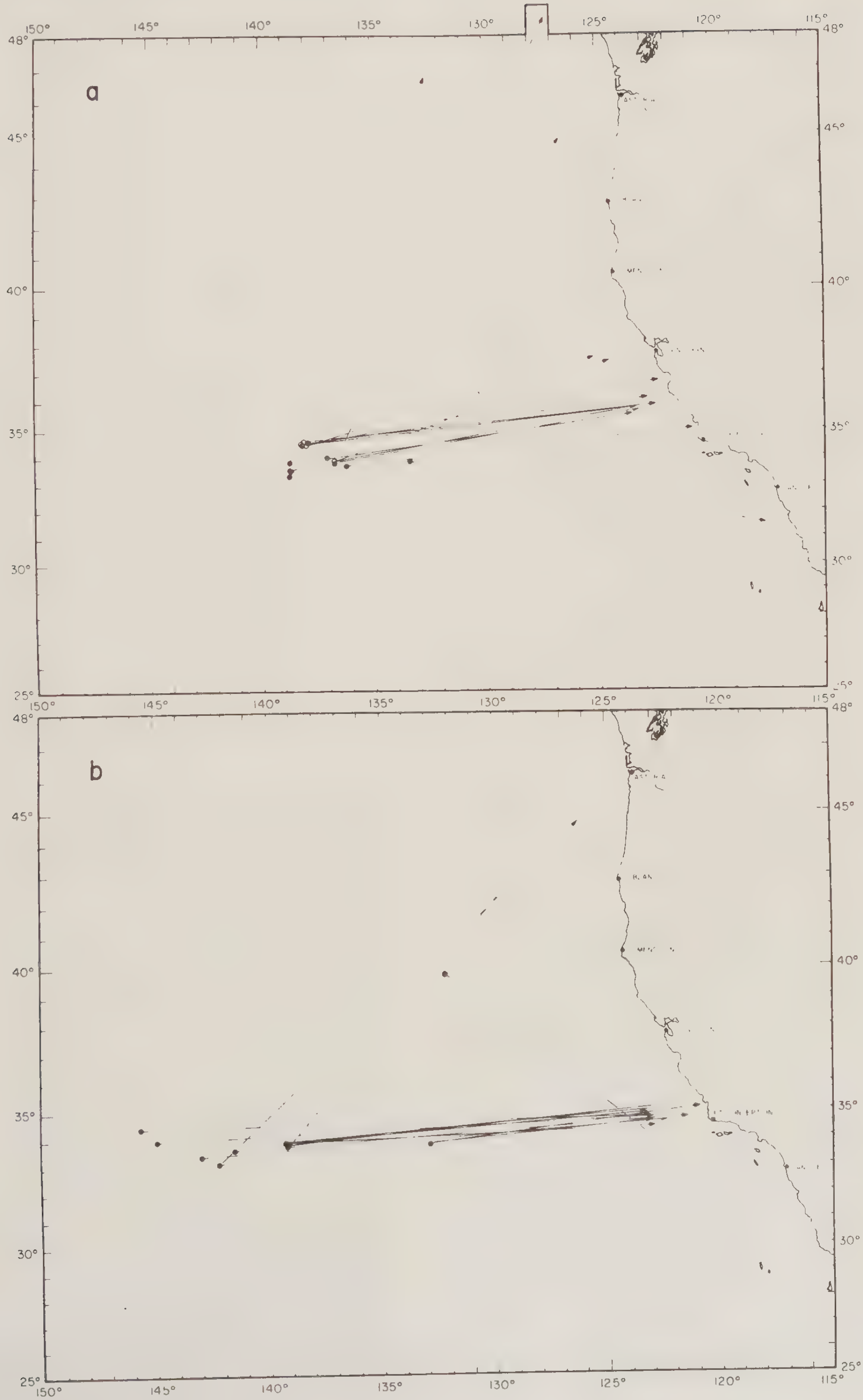
MIGRATION PATTERN FROM OFFSHORE TO NEARSHORE WATERS

We view the general pattern of seasonal migration of albacore into coastal waters where the U.S. fishery traditionally takes place during summer-fall as proceeding in three main stages: First, albacore migrate eastward from central North Pacific regions and form centers of high relative abundance within the eastern sector of the Transition Zone waters 600 to 1,000 mi off the coast. This development initially occurs in late May and June, a time when seasonal warming has raised the surface layer temperature of these waters to values considered to be within the habitat preference for albacore. These concentrations of fish may persist in offshore waters for several weeks. Next, as nearshore waters warm in ensuing weeks, albacore migrate toward coastal regions. Fishing efforts in the intervening zone usually produce only scattered catches, thus suggesting that during the shoreward migration the behavior of the fish is such that they are not available to fishing gear and/or that albacore may not be concentrated. Then, usually by mid-July, concentrations of high relative abundance are found near the coast, often in the vicinity of oceanic fronts related to coastal upwelling. Although variations may occur in this general pattern, the main features of the migration tend to repeat each year. The stages of shoreward migration and initial development of the albacore fishery can be seen in the two series of charts showing nominal catch per unit effort for 1973 (Figures 5a-e, 6a-e).

The shoreward migration of albacore from the central North Pacific into coastal waters appears to continue through the summer months. Albacore trolling experiments conducted from U.S. Navy picket vessels operating approximately between long. 130° and 135°W (Flittner 1963, 1964) showed albacore to be available there throughout the summer. Also, two albacore tagged by the Japanese in the western Pacific (near lat. 35°N and long. 171°E) in mid-June 1974 were recovered in the U.S. fishery in September 1974 (Japanese Fisheries Agency 1975).

Division in Migration Pattern

In order to examine migration of albacore from offshore to nearshore waters, an albacore tagging program was conducted during each of the offshore surveys. Over 4,500 albacore were tagged and released (Table 1). Recoveries of tagged fish made during the same season as released provide information on migration of albacore into nearshore waters (Figure 11a-c). Most recoveries of tagged fish made in 1972 of fish tagged during early season 1972 in waters offshore of long. 130°W were made in central-southern California waters and only a few recoveries were made in Pacific Northwest waters (Figure 11a). A similar recovery pattern was observed in 1973 (Figure 11b). A contrasting recovery pattern was observed in 1974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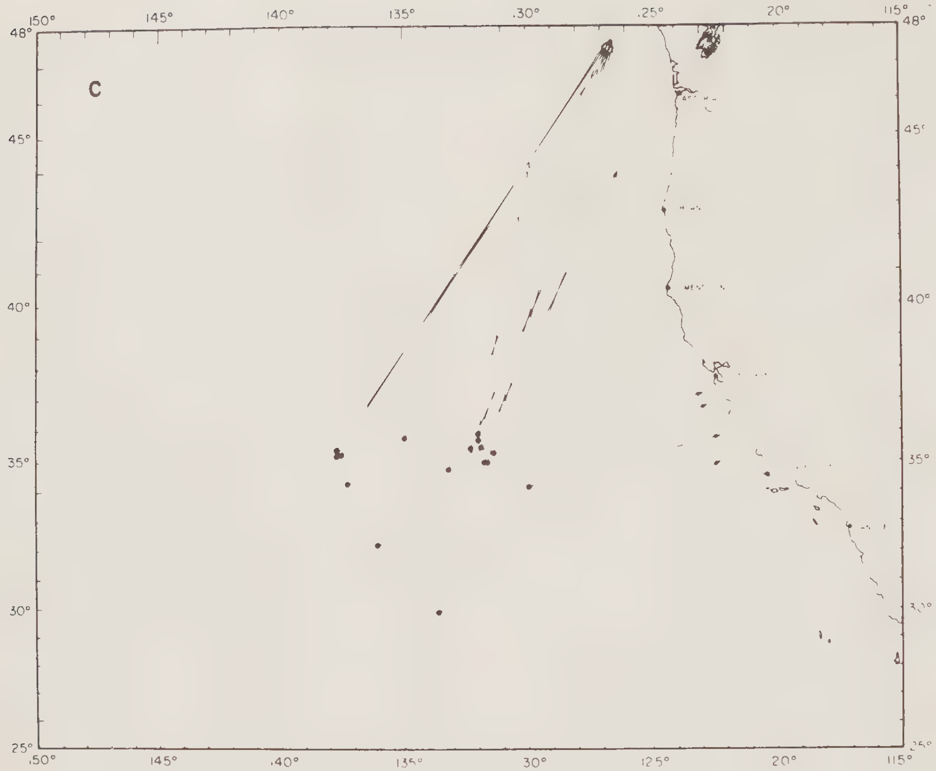

FIGURE 11.—Recoveries made during the same season as release of fish tagged during the early-season surveys in: a. 1972; b. 1973; and c. 1974.

when almost all of the recoveries of fish tagged in 1974 were made in waters off the Pacific Northwest (Figure 11c).

Differences in recovery pattern cannot be accounted for by geographic variations in fishing effort and fish catch. In all 3 yr, 70% or more of the fish caught during the commercial fishery was off the Pacific Northwest. It appears, instead, that differences in recovery patterns could be related to the location where tagged fish were released. In both 1972 and 1973, most of the tagging effort in offshore waters was between lat. 33° and 34°N and in 1974 it was farther north, between lat. 35° and 36°N. The different and divergent patterns apparently are the result of the albacore following different and divergent migration routes toward the nearshore waters. Tagging efforts of 1972 and 1973 and those of 1974 were apparently concentrated upon different branches of the migration. The division in the migration pattern appears to have occurred near lat. 35°N and must have occurred west of, and prior to, the appearance of the fish in the survey region.

Support for this proposed division in the migration pattern of albacore is indicated by differences in length-frequency distribution of albacore caught in the commercial fishery off California and north of California. Differences in size composition of fish caught in 1972 in the two regions (Figure 12 upper and lower) include: 1) the mode of large-size fish was about 5 cm larger in fish caught off California than in fish caught off the Pacific Northwest; 2) the mode of the medium-size fish, which formed the dominant size group in both regions, was 1 to 2 cm larger in fish caught off California than in fish caught off the Pacific Northwest; and 3) occurrence of three modal size groups taken in the fishery off California, but only two off the Pacific Northwest, where the smallest modal size group was absent. Examination of size-frequency distributions for 1973 and 1974 yielded similar results.

The size composition of albacore caught west of long. 130°W by charter vessels in 1972 (Figure 12 lower) was very similar to that for fish taken in the commercial fishery off California (Figure 12 mid-

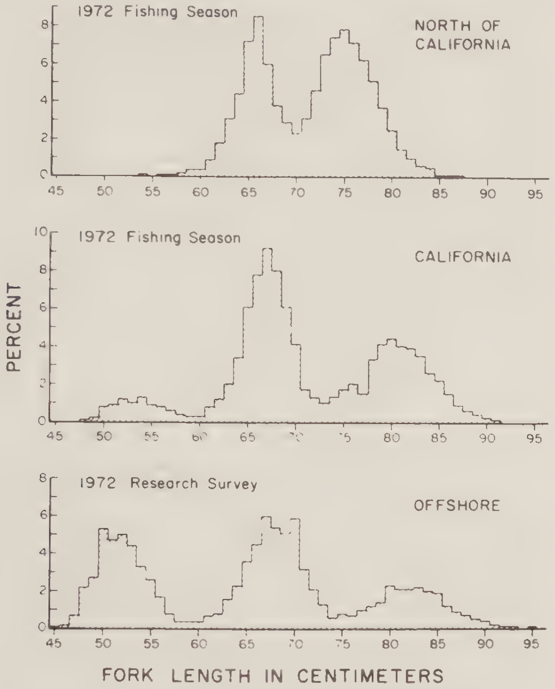

FIGURE 12.—Size composition of albacore caught by U.S. fishermen during 1972 north of California (upper), off California (middle), and size composition of albacore caught during the 1972 National Marine Fisheries Service-American Fishermen's Research Foundation offshore survey (lower).

dle) and hence different from the size composition of fish taken in the commercial fishery north of California (Figure 12 upper). It appears, then, that albacore caught in the offshore region of high relative abundance south of lat. 35°N in 1972 were a part of the migration of fish that reached regions off California.

We interpret the findings concerning offshore-nearshore and north-south geographic variations in size composition as supporting the hypotheses 1) that the fish which compose the fishery off California are separate from those which make up the fishery off the Pacific Northwest, and 2) that these two groups of fish follow different migration routes into nearshore waters.

Movements of Albacore by Size Groups

The size composition data for the 1972 charter vessel catch were stratified into offshore and nearshore regions at long. 130°W and into one 8-day and four 10-day time periods. Graphs of the stratified data standardized by fishing effort for 1972 (Figure 13) show that albacore initially appeared offshore near the end of May and there was an abrupt increase in relative abundance in the beginning of June. A decline in relative abundance was observed offshore after 19 June as centers of abundance shifted to nearshore where there was an increase in early July. Within these overall trends, changes in each of the three modal size groups can be followed. The mid-size modal group (fork length centered about 67 to 69 cm), initially dominated early offshore catches and then diminished in relative importance. It formed almost the entire catch of the first nearshore catches and continued to dominate nearshore catches into July. The large-size modal group (fork length centered about 82 to 85 cm) showed similar trends: a rise and fall in relative abundance offshore and with a subsequent shift to nearshore, but lagging behind the mid-size modal group by one 10-day period. The small-size modal group (fork length centered about 52 and 53 cm) was dominant offshore after 10 June but made little appearance in the nearshore region during the survey. This size group subsequently entered the nearshore fishery, however, as is evident from the size composition of the 1972 fishery off California (Figure 12 middle). An additional geographic division in

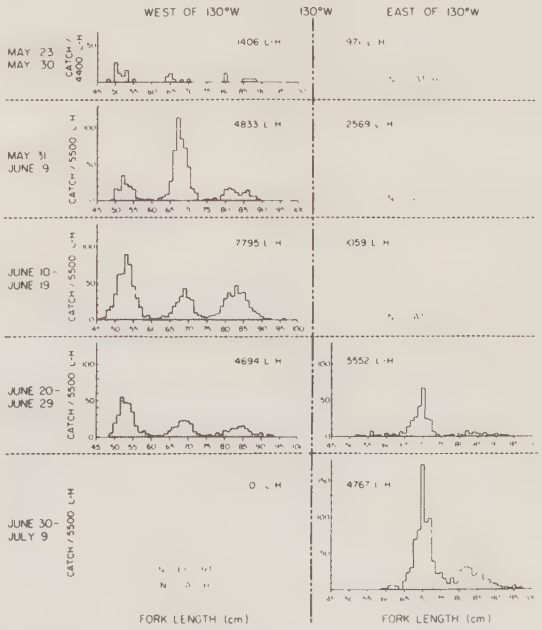

FIGURE 13.—Size composition of albacore caught by American Fishermen's Research Foundation charter vessels in 1972 by time periods and east and west of long. 130°W.

the offshore region, splitting the catch north and south of lat. 35°N showed that the catches first developed south of lat. 35°N and then moved north. By the fourth period (20 to 29 June), the small-size modal group composed almost the entire catch south of lat. 35°N and offshore of long. 135°W.

Several conclusions are evident from these temporal and areal changes in size composition. While catches persisted for up to 4 wk within a 2° by 4° quadrangle of latitude and longitude in the offshore region, changing patterns of size composition suggest that albacore were moving through the region within a period of 10 days or less and that the size groups migrated somewhat independently. The mid-size group, which composes the major portion of the U.S. fishery, led other size groups by 10 or more days. Also, the sequence of compositional changes of each size group and the geographic differences suggest that the migration from the offshore region to the nearshore fishery takes about 20 days or more; at least it did in 1972.

The 1972 catch data were chosen for examination of spatial and temporal changes in size composition because each of the size groups was well represented in the survey catches and all phases of the migration into the fishery are evident, including commencement of the fishery, by the completion of the survey. In 1973 the fishery started late, weeks after the survey, and in 1974 the patterns were less distinct, apparently in response to weak oceanic frontal conditions.

DISCUSSION

Association of Albacore Distribution With Oceanic Frontal Regions

The commercial fisheries on North Pacific albacore and the migration of albacore among these fisheries have frequently been associated with oceanic frontal regions in the western Pacific (Yamanaka et al. 1969; Uda 1973; other works), in the central North Pacific (Shomura and Otsu 1956; McGary et al. 1961), and in coastal upwelling regions (Pearcy and Mueller 1970; Panshin 1971; Laurs 1973; Laurs et al. 1977).

Results of our study provide evidence for the continuity of the association of albacore distribution with the Transition Zone and frontal boundaries into the eastern North Pacific. Catches made by the AFRF charter fishing vessels and the research vessel during each of the three surveys demonstrate that albacore are distributed mainly within the Transition Zone and usually are absent (or unavailable) in water masses to the north and south. Furthermore, our work strengthens the general concept that the distribution and relative abundance of large, highly migratory fish may be markedly influenced by oceanic frontal features. Other studies usually have had to rely on mean ocean conditions and/or statistically averaged fishery data, whereas our fishery and oceanographic data were collected concurrently during several surveys, and the amounts of fishing effort, fish catch, and oceanographic data were substantial.

Relative Abundance of Albacore in the Eastern Sector of the Transition Zone

We have found centers of high relative abundance of albacore in June within the eastern sector of the Transition Zone and often close to its frontal boundaries. Annual and intra-annual areal variations in relative abundance of albacore were observed and appeared to be related to development of the frontal boundaries of the Transition Zone. When the Subarctic and Subtropic fronts were strongly developed, areas of high relative abundance developed within relatively narrow bands in the Transition Zone and persisted for several weeks. When the Transition Zone was broader and the fronts were poorly developed, centers of high relative abundance were found over a larger area within the Transition Zone and did not persist for more than several days in any one location.

Based on scouting results from several research surveys, it appears that the timing and the location of fishing effort may be critical in locating centers of high relative abundance of fish in the eastern sector of the Transition Zone. In 1973, charter vessels first found a center of high relative abundance on 4 June near lat. 34°N, long. 140°W in Transition Zone waters. For several weeks prior to this finding, the AFRF charter vessels had made only scattered catches while scouting in and about this same area. Thus, it seems that the center of high relative abundance appeared in a surge within the first week of June. In 1955, an albacore survey cruise by a single U.S. Bureau of Commercial Fisheries (BCF) research vessel (*Hugh M. Smith*) scouted this area in late May and early June (Graham 1957). Seven longline sets and trolling conducted between lat. 41° and 28°N along long. 139°W resulted in only a single albacore being taken before the vessel departed the area on 5 June. The 1955 scouting effort may have been too early by a matter of days to weeks to locate substantial numbers of fish. In 1957, a BCF fishery research vessel (*John R. Manning*) scouted to the north and east of this area in late June (Callaway and McGary 1959). Small to modest catches of albacore were made by trolling and in gill net sets in and about the Transition Zone, but the area which we have found to have a center of high relative abundance was not scouted.

Extension in Space and Time of U.S. Albacore Fishery

The cooperative NMFS-AFRF albacore research surveys have demonstrated the feasibility of extending the U.S. fishery for albacore in space and time. Albacore were caught by chartered fishing vessels in commercial concentrations considerably farther offshore than where the albacore fishery has traditionally taken place and up to 6 wk prior to the usual beginning of the fishing season. Noncharter commercial albacore fishing vessels, attracted to the early season offshore fishery by the research survey findings, have begun operating in this fishery in increasing numbers.

While fishing results of the AFRF-chartered and the nonchartered fishing vessels indicate that commercial amounts of fish can be caught earlier and farther offshore than the usual fishing season, additional experience is needed to examine the variability of this extension of the fishery, especially in terms of timing and availability, in order to judge properly whether it can provide a dependable contribution to the U.S. fishery. If in the long-run the early season offshore fishery proves viable, its development could be an important factor in reducing annual fluctuations in the catch of albacore. According to Clemens (1962) large annual fluctuations in catch are a prominent feature of the U.S. albacore fishery. Stabilization of catch among years could contribute significantly to the proper utilization and ultimately to the effective management of the resource.

The fishing success by charter and noncharter albacore commercial fishing vessels in 1972-74 is in contrast to an earlier attempt to establish commercial fishing in waters offshore from where the U.S. fishery has historically operated. According to McGary et al. (1961), an unsuccessful gill net and trolling effort was made in the summer of 1958 by a chartered commercial fishing vessel in areas of the central North Pacific where albacore were caught during research surveys conducted in summers of 1955 and 1956. The failure to catch albacore in amounts sufficient to support commercial fishing may have been an accidental event related to intense anomalous oceanic conditions which occurred ocean-wide and affected numerous fisheries in 1957-58 (Sette and Isaacs 1960).

Association of Shoreward Albacore Migration With Transition Zone and Possible Mechanisms

Shoreward Migration and Transition Zone

Based on association of albacore distribution and relative abundance with the Transition Zone and its frontal boundaries, we conclude that the shoreward migration of albacore is linked to the Transition Zone and that variations in the pattern of migration occur in response to variations in the character and development of the Transition Zone and its frontal structure. When the Transition Zone is narrow and its fronts are well developed, as in 1972 and 1973, the migration pattern of the fish is narrow and relatively well defined. In contrast, when the Transition Zone is broad and its fronts weakly formed, as in 1974, the migration pattern of fish is wide and less well defined.

There is also some suggestion that the strength and continuity of the Transition Zone fronts in offshore waters may affect the timing of arrival of fish in nearshore waters. When the fronts are well developed, fish appear to aggregate in their vicinity, resulting in a tendency for the fish to remain in offshore waters for periods of time that delay their arrival in the nearshore fishing grounds. However, when the fronts are weak the fish appear to move through offshore waters with less delay and arrive earlier in nearshore waters. Initial showing of fish in nearshore waters during the years of the surveys supports this speculation. The nearshore commercial fishery and sport fishery off southern California commenced several weeks later in 1972 and 1973 than in 1974.

Possible Mechanisms for Association of Albacore With the Transition Zone

The mechanisms responsible for the relationship between albacore and the Transition Zone and its frontal boundaries may result from a number of factors acting in an interrelated matrix which impacts the fish both directly through physiological means and indirectly through forage availability. We postulate that the factors include, but are probably not limited to: 1) habitat temperature preference, 2) biological productivity, and 3) thermal gradients as they affect the albacore's thermoregulation processes, and that these factors act in an interrelated way superimposed on the innate drive of the fish to migrate across the North Pacific Ocean.

HABITAT TEMPERATURE PREFERENCE. — The distribution and relative abundance of albacore are related to sea-surface temperature (Clemens 1961; Johnson 1962; Panshin 1971; and others). The habitat temperature preference for albacore ranges from approximately 16° to 19°C (Clemens 1961; Laveastu and Hela 1970). This temperature range is found in the upper mixed layer waters of the Transition Zone in spring. Near-surface waters to the south of the Transition Zone are generally warmer than this and those to the north cooler.

The sequence of spring-summer warming of the surface layer along a section between Honolulu and San Francisco during 1972 is illustrated in Figure 14. The Transition Zone boundaries identified by the abrupt changes in depth of isotherms at intermediate depths fall between long. 130 and 140° W. The habitat temperature preference range for albacore (16° to 19°C) is shown with shading. In early and mid-spring (upper left) only the Central waters have preferred temperatures and these waters occur down to a considerable depth, almost 200 m. In subsequent time periods, a shallow sur-

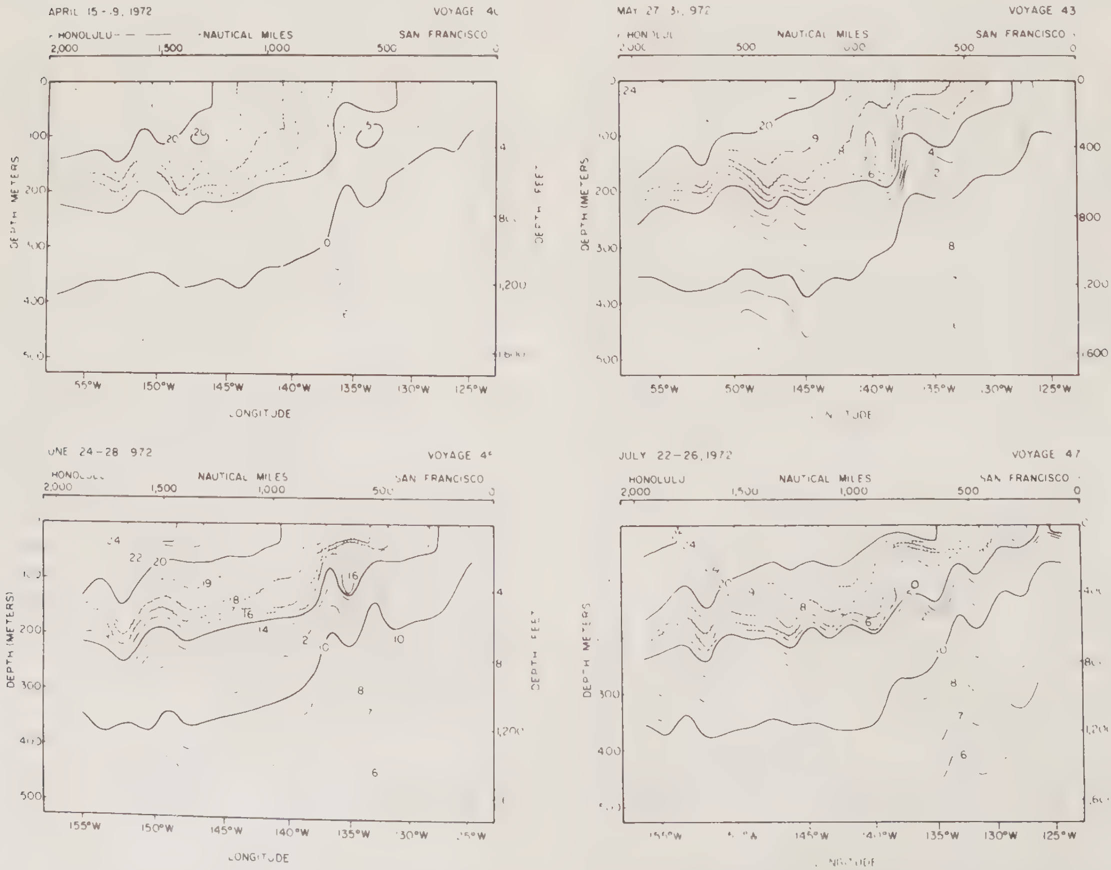

FIGURE 14.—Vertical temperature sections on a transect from Honolulu to San Francisco during April to July 1972. The temperature range between 16° and 19°C (60.8° and 66.2°F) is shaded.

face layer develops and warms to preferred temperatures, initially in the Transition Zone and then in more nearshore waters. It is near the end of May and through June that the preferred temperature range occurs in the Transition Zone and is generally restricted to depths ~70 m. The depth limitation of preferred waters greatly improves the vulnerability of albacore to surface trolling gear.

BIOLOGICAL PRODUCTIVITY.—Tagging data show that migration of albacore from the western to the eastern North Pacific is active with an average migration speed of 48 km/day for 78- and 80-cm fish (Japanese Fisheries Agency 1975). This suggests that an albacore requires considerable energy to complete the transpacific migration. Sharp and Dotson (1977) calculated that the caloric expenditure per hour for a swimming albacore 63 cm in fork length is 5.02 kcal/h. They also speculated that fat stores may be an important energy source utilized by albacore for migration. Studies of the food habits of albacore caught during the surveys[11] show that albacore feed actively in offshore waters during their shoreward migration. The composition of the food found in the stomachs is different from that of fish caught in inshore waters (Pinkas et al. 1971, Laurs and Nishimoto MS[12]), but average volumes of food in stomachs from the two regions are similar. Therefore, availability of forage is likely to be an important factor influencing the route of albacore migration.

There are three major oceanic habitats in the North Pacific which are separated by pronounced latitudinal faunal boundaries and steep latitudinal gradients in standing stocks of phytoplankton and zooplankton (McGowan and Williams 1973). These species and biomass boundaries are coincident with the boundaries of the Pacific Subarctic, Transition Zone, and Pacific Central waters (Johnson and Brinton 1963). A northward increasing step-cline occurs among the North Pacific habitats in standing stocks of phytoplankton (Venrick et al. 1973; McGowan and Williams 1973), zooplankton (Reid 1962; McGowan and Williams 1973), and micronekton (Aron 1962), and in primary production (Koblents-Mishke 1965). Zooplankton and micronekton standing stock estimates made during the offshore albacore surveys show similar results with values generally being highest in Subarctic waters, intermediate in Transition Zone waters, and lowest in Central waters.

Since biological productivity is higher in Subarctic waters than in Transition Zone or Central waters, it would be most advantageous from the standpoint of food availability for albacore to confine their migration path to Subarctic waters. However, during spring months the temperature of the Subarctic waters is much lower than the habitat preference for albacore. We conclude, then, that the northern limit of the albacore migration route during spring is determined by ocean temperature and that the limiting temperature is found near the northern boundary of the Transition Zone. The temperature of the upper layer of the Central waters is higher than the habitat temperature preference for albacore, but there are temperatures below the upper layer which lie within the habitat temperature preference for albacore. Thus, temperature could restrict the distribution of albacore from the upper layer but not at some depth interval below the upper layer. We propose that while temperature may play a role in determining the southern limit of the albacore distribution and migration route, the major factor is the abundance and availability of forage organisms which drop off sharply near the southern boundary of the Transition Zone.

OCEAN THERMAL GRADIENTS AND THERMOREGULATION OF ALBACORE.—Thermoregulation processes by albacore may be an important factor in determining their association with the Transition Zone and its frontal boundaries. Thermoregulation is characteristic of tunas and certain other fishes (Carey et al. 1971). According to Neill (1976) for fishes as a group, the only effective means of regulating body temperature is by behavioral regulation of the immediate environmental temperature through locomotory movements.

Computer simulation models developed by Neill (1976) indicate that where environmental conditions are characterized by large expanses of isothermal or nearly isothermal water separated by relatively narrow thermal discontinuities (e.g., oceanic frontal systems), fishes will be relatively concentrated near the discontinuities.

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[11] Laurs, R. M., and R. N. Nishimoto. 1973. Food habits of albacore caught in offshore area. *In* Report of joint National Marine Fisheries Service-American Fishermen's Research Foundation albacore studies conducted during 1973, p. 36-40. (Unpubl. rep.)

[12] Laurs, R. M., and R. N. Nishimoto. Food habits of albacore in the eastern North Pacific. (Unpubl. manuscr.)

Division in the Migration of Albacore Into the American Fishery

Our study indicates that there is a division in the migration pattern of albacore into the American fishery with fish which compose the fishery off the Pacific Northwest and off California following different routes. We believe that the "northern" branch of the migration progresses as described by Powell et al. (1952) who, during an exploratory albacore fishing survey over a region off the Pacific Northwest, found albacore along a warm-water edge that develops seasonally 400 to 500 n.mi. offshore of southern Oregon in late June and early July. The warmwater edge was observed to progress northward and coastward in a bulge or pouchlike pattern as seasonal warming of the surface waters took place over the ensuing weeks. The occurrence of albacore was found to follow the progression of the warmwater zone shoreward and northward along the coasts of Oregon and Washington and by mid-August to waters off the Queen Charlotte Islands, British Columbia. Powell et al. (1952) concluded that these findings, as well as earlier observations, indicated that the main barrier directly or indirectly influencing the distribution of albacore throughout their northern range is water temperature.

Clemens (1961) investigated the onset and movements of the albacore fishery off California and Baja California for the fishing seasons 1951 through 1953. From catch records he found that albacore entered the coastal waters as far south as 200 n.mi. south of Guadalupe Island (lat. 29 N) in some years and as far north as the San Juan Seamount (lat. 33 N) in others. He also presented tag recovery data which showed that albacore move from Baja California or southern California in the early season northward to central California as the season progresses (however, only one recovery of a tagged fish was made off northern California). Clemens concluded that albacore entering the American fishery initially migrate to Baja California or southern California and that longshore movement was the dominant mode of their dispersal into coastal zones to the north. Although he allowed that albacore may reach Oregon and Washington waters by following the seasonal bulge of warm offshore water as suggested by Powell et al. (1952), Clemens stated that a large part of the main body of albacore travel northward up the coast to waters off the Pacific Northwest from Baja California and southern California. No evidence was given for this statement and our newer findings do not support it. We concur that northward longshore movement is important in nearshore waters, but conclude that fish entering waters off Baja California or southern California do not migrate farther north than about San Francisco before leaving the American fishery.

Flittner (1963) presented a schematic diagram of albacore movement off the Pacific coast based on albacore catches made by U.S. Navy picket vessels during 1960-62. The picket vessels, stationed 200 to 500 n.mi. offshore (no farther west than long. 135 W) and spaced at latitudinal intervals of 300 n.mi., each trolled several jig lines from May through October. Flittner said that albacore appeared to congregate within an "optimum-temperature" zone and seem to split into two migratory components. Early arrivals proceed to southern feeding areas and late arrivals turn to the northern area, each movement depending upon the progression of seasonal warming.

Progression of seasonal warming continues to appear to be an important factor affecting paths of albacore migration. However, influence of the Transition Zone development and the division of migration pattern described here add considerable complexity to earlier ideas. Our findings suggest that events in offshore waters are important in determining the distribution and relative abundance of albacore in coastal waters.

Pacific Northwest and California Groups of Fish

Based on offshore-nearshore and north-south geographic variations in size composition of albacore we postulate that the group of fish which compose the albacore fishery off California are separate from those which make up the fishery off the Pacific Northwest. Brock (1943) arrived at a similar conclusion after comparing length-frequency distributions of albacore landed in San Pedro, Calif., and Astoria, Oreg. Brock found differences in size composition and stated, "This would argue that the schools of fish off the Oregon coast were not a part of the schools appearing off the California coast, even though, as indicated above, the two groups may have had a common origin. . . The time of arrival of fish and their abundance as shown by the monthly commercial catch for the ports discussed here (San Pedro and Astoria) make it seem likely that at least two separate groups of schools invaded the coastal area, one in the north off Oregon and the other in the south off southern California."

Results of studies on the artificial radionuclide ^{60}Co in albacore provide additional evidence that the "northern" and "southern" groups of fish are independent. Krygier and Pearcy (1977) found that the peak activity levels of ^{60}Co in albacore off Oregon occurred a year earlier than the peak activity levels seen by Hodge et al. (1973) off southern California. According to Krygier and Pearcy, the heaviest fallout input of ^{60}Co into the North Pacific occurred at about lat. 40°N. They speculated that due to circulation in the North Pacific, albacore which were associated with waters north of lat. 35°N could have experienced high levels of ^{60}Co up to a year before the tuna associated with waters to the south. They concluded that, "Circulation in the North Pacific and the latitudinal differences in the location of the two portions of the albacore population [as proposed by Laurs and Lynn in this paper] appear to be a plausible explanation for the difference of 1 yr in activity peaks between albacore caught off Oregon by us and those off southern and Baja California by Hodge et al. (1973)." Thus, strong evidence from several independent sources points toward two separate groups of albacore following separate migration paths.

ACKNOWLEDGMENTS

We thank the American Fishermen's Research Foundation for their farsighted interest and their support for albacore and oceanographic research (particularly, in this regard, Robert Insinger and John Bowland). We owe a debt of gratitude to the captains and crews of the RV *Townsend Cromwell* and *David Starr Jordan*, and the chartered fishing vessels, and to the staff of the Albacore Fishery Investigations whose loyal support and perserverance made this work possible.

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8. ALBACORE ADVISORY PROGRAMME AT THE SOUTHWEST FISHERIES CENTER, LA JOLLA, Ca., U.S.A.

by

R.M. Laurs

8.1 Introduction

The National Oceanic and Atmospheric Administration, National Marine Fisheries Service (NOAA/NMFS), La Jolla Laboratory (and predecessor organizations) has operated an albacore fishery forecasting/advisory services programme since the early 1960's. For the past several years this programme has been a sub-unit of a multidisciplinary research programme on North Pacific albacore, intended to develop optimal management policy recommendations with respect to U.S. interests in North Pacific albacore fisheries and to produce information for optimal planning and operating decisions in the U.S. albacore industry.

8.2 Users of fishery forecast/advisory materials

The users of the albacore fishery forecasting/monitoring services are many and varied. Strategic forecast materials are being used by

- the commercial albacore fishing industry, especially the fish processing and wholesaling components, and operators and owners of fishing vessels or fleets of fishing vessels;
- the recreational fishing community, notably operators of charter boats;
- the management agencies of the State and (potentially) Federal governments.

Tactical fishery forecasting/monitoring materials are used mainly by

- the U.S. albacore jigfishing and baitboat fishing fleets, fish buying stations and other components of the industry;
- recreational albacore fishermen;
- resource managers

The needs of the U.S. albacore tuna fishing industry and fishery managers for strategic and tactical fishery forecasting/monitoring services have been specified through dialogues with members of various components of the industry and fishery scientists, and in literature. A re-evaluation of the needs of the user groups is periodically required due to changes in the fisheries for North Pacific albacore. For example, information on fleet allocation will no doubt need to be added to the strategic list of needs of the U.S. industry.

The strategic needs of all user groups are on time-scales of up to several forthcoming seasons and on an ocean-area basis space-scale. The strategic needs include: (i) the general area in which the stock of fish will be available in the forthcoming season relative to its area of availability in the long-term, specifically the seasonal geographic location of centers of the fishery, e.g., north-south and nearshore-offshore; (ii) range of the fishery in time and space; (iii) the probable level of abundance of the stock of fish over the fishery area in the forthcoming season, relative to its long-term abundance; (iv) variation in expected size composition of fish; (v) the probable long-term oceanographic conditions which may affect fishing operations due to predicted broad-scale anomalies, specifically information on general ocean surface and subsurface temperature conditions; and (vi) the probable long-term wind and sea conditions which may affect fishing operations by broad area due to predicted climatic anomalies.

The tactical needs of all the user groups are similar to the strategic needs, but on time-scales of a few days or weeks and on a "local" area space-scale.

8.3 Albacore fishery forecast advisory/materials

8.3.1 Seasonal forecast

The seasonal forecast is issued in early June about 4 to 6 weeks before the usual beginning of the fishing season. The basic elements of the forecast include a) the proportions of the total catch that are expected to be caught off the Pacific Northwest and off California (north and south of San Franciso), b) an account of trends in oceanographic and atmospheric conditions as they pertain to "set-up" conditions for the forthcoming season, c) long-range outlook of oceanographic, atmospheric and weather conditions that may affect the fishery, and d) information on the catches and landings by state for prior and recent years.

The prediction of the percentages of the seasonal catch expected to be taken north and south of San Francisco is based on an index which qualitatively relates the north-south geographic distribution of albacore catch with oceanographic conditions during spring months in offshore waters through which albacore immigrate to the North American West Coast. In addition, relationships between geographic shifts in the fishery, including oceanographic frontal boundary features, geographic trends in catch and, to a lesser degree, the nearshore ocean conditions and projected distribution of atmospheric conditions are used. The discussions of trends in oceanographic and atmospheric conditions are based on analyses conducted at the La Jolla Laboratory. The long-range outlook for oceanographic conditions that may affect the fishery is based on an evaluation of recent trends in broad-scale anomaly patterns and the probable effects that the long-range atmospheric conditions will have on oceanographic conditions. The projection of long-range weather conditions is obtained from the National Weather Service.

8.3.2 Biweekly fish bulletins

Albacore fish bulletins (Figure 1a and b) are issued in conjunction with 15-day sea surface temperature charts (see below). Included in the bulletins are short-term projections of albacore distribution and locations of productive fishing areas, information on oceanographic and meteorological conditions, and other information as appropriate. The bulletins are mailed to fishermen and others upon request and are bulk-mailed to fish buyers and processors for further dissemination to fishermen. The bulletins are based on fishery information radioed ashore from cooperating fishermen, from fish buyers and processors, fishermen's associations, and State fishery agencies. Oceanographic information is based on analysis of ocean conditions conducted at the La Jolla Laboratory and an extended weather forecast is provided by the National Weather Service.

8.3.3 Albacore fishing information daily forecasts

Daily broadcasts of albacore fishing information are prepared by the La Jolla Laboratory staff and transmitted to the fishing fleet at sea. The broadcasts include the latest albacore fishing information obtained from research vessels, cooperating fishing vessels, unloading station operators, processors, fishermen's foundations and State fishery agencies. Highlights include location of active centres of fishing, typical fishing scores, size of fish, sea surface temperature and subsurface temperature information when available, and other information as appropriate. A weather and sea state summary prepared by the National Weather Service is also given, including large-scale weather features, regional wind, weather and sea state conditions between 20-250 miles offshore, and storm development. The broadcasts are made twice daily on weekdays and once on Saturday mornings during the albacore fishing season. The broadcasts are transmitted by radio station WWD which is licensed to the National Marine Fisheries Service and Coast Guard radio station NMC on several single side band frequencies and by a number of commercial radio stations along the U.S. Pacific coast on commercial AM frequencies.

8.3.4 Oceanographic advisory information

(i) Biweekly sea surface temperature (SST) charts

The biweekly SST charts cover the area between central Baja California, Mexico and Vancouver Island, British Columbia, Canada out to 135°W (see R.H. Evans, section 7, Figure 1). The SST charts are distributed year-round, but during the albacore fishing season, from about July through October, they are included with the Albacore Fish Bulletins described in section 8.3.2. R.H. Evans gives additional information concerning the SST charts.

(ii) Weekly sea surface temperature (SST) charts

The weekly SST charts cover the same area as the biweekly charts and are transmitted by radio station WWD via radiofacsimile to albacore fishing vessels on the fishing grounds each Friday during the fishing season. Approximately 25 albacore vessels are fitted with radiofacsimile recording equipment. These vessels often pass information on SST gained from the charts to other vessels via voice radio communication.

8.4 Additional information

8.4.1 Vertical sections of ocean temperature

Vertical profiles of ocean temperature and surface temperature and salinity observed between the U.S. west coast and Hawaii (Figures 2a and 2b) have application to the U.S. albacore fishery. The subsurface temperature structure is made from expendable bathythermograph (XBT) drops by cooperating merchant vessels; surface temperature and salinity observations are also made at each XBT station[1] (Saurs and Stevens 1972). The charts are published monthly in Fishing Information. In recent years there has been an expansion in the albacore fishery to much farther offshore and about 2 months earlier than the historical start of the fishing season. Fishermen have used the vertical thermal profiles and accompanying information to assist in planning strategy for fishing in the offshore waters during the early season. The isotherms between 16° and 19°C are shaded as an aid to follow variations in distribution of these isotherms which are within the habitat temperature preference for albacore. The charts can also be used to locate oceanic boundary features where the relative abundance of albacore has been found to be high in offshore waters (Laurs and Lynn, in press).

8.4.2 Charts of nominal CPUE and size composition

As an incentive for fishermen to keep logbooks, charts showing nominal catch per unit effort summarized by 15-day period and 1° quadrangle (Figure 3) and size composition by area (Figure 4) for the preceding season are distributed to fishermen with logbooks for use during the forthcoming season. The charts are issued as cooperative products of the state fishery agencies and NMFS. The processing, standardization, and management of a uniform U.S. West Coast logbook for albacore (Laurs, Hooker, Hreha, and Lincoln, 1975) are shared by the states and NMFS. Processing, including editing and quality control, is accomplished by state fishery personnel. The data from each of the states are then made available to the La Jolla Laboratory in ADP form. NMFS scientists merge the data from the states, and the fishing effort is standardized using a modified version of the computer programme FPOW (Berude and Abramson, 1972) as described by Laurs, Clemens, and Hreha (1976).

Comments received from fishermen indicate satisfaction with the CPUE and size composition charts. According to some fishermen, they are more conscientious in keeping logbooks because of the receipt of the catch charts.

1/ Data are processed under supervision of personnel at NMFS Pacific Environmental Group, Monterey, California, using computer facilities of the Navy Fleet Numerical Weather Central, Monterey, California. The project is partially supported by the National Science Foundation and Office of Naval Research

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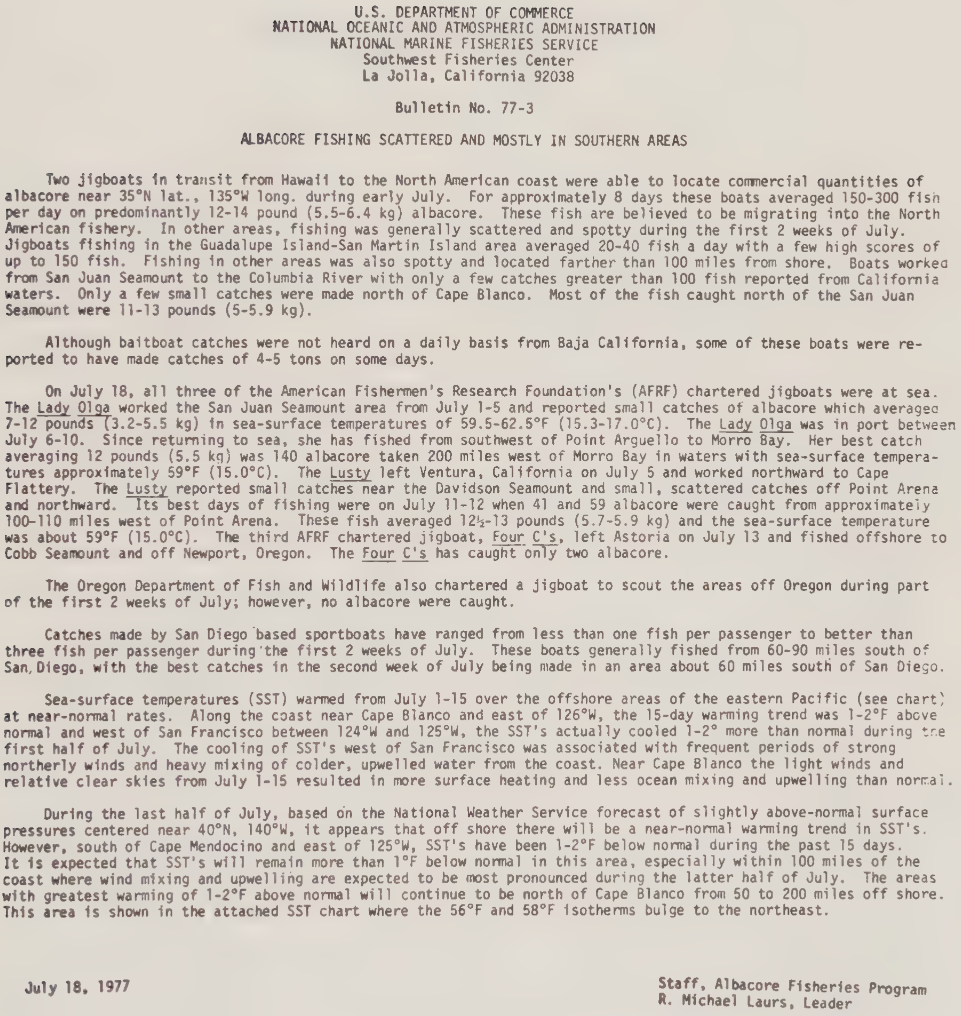


U.S. DEPARTMENT OF COMMERCE
NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
NATIONAL MARINE FISHERIES SERVICE
Southwest Fisheries Center
La Jolla, California 92038

Bulletin No. 77-3

ALBACORE FISHING SCATTERED AND MOSTLY IN SOUTHERN AREAS

Two jigboats in transit from Hawaii to the North American coast were able to locate commercial quantities of albacore near 35°N lat., 135°W long. during early July. For approximately 8 days these boats averaged 150-300 fish per day on predominantly 12-14 pound (5.5-6.4 kg) albacore. These fish are believed to be migrating into the North American fishery. In other areas, fishing was generally scattered and spotty during the first 2 weeks of July. Jigboats fishing in the Guadalupe Island-San Martin Island area averaged 20-40 fish a day with a few high scores of up to 150 fish. Fishing in other areas was also spotty and located farther than 100 miles from shore. Boats worked from San Juan Seamount to the Columbia River with only a few catches greater than 100 fish reported from California waters. Only a few small catches were made north of Cape Blanco. Most of the fish caught north of the San Juan Seamount were 11-13 pounds (5-5.9 kg).

Although baitboat catches were not heard on a daily basis from Baja California, some of these boats were reported to have made catches of 4-5 tons on some days.

On July 18, all three of the American Fishermen's Research Foundation's (AFRF) chartered jigboats were at sea. The Lady Olga worked the San Juan Seamount area from July 1-5 and reported small catches of albacore which averaged 7-12 pounds (3.2-5.5 kg) in sea-surface temperatures of 59.5-62.5°F (15.3-17.0°C). The Lady Olga was in port between July 6-10. Since returning to sea, she has fished from southwest of Point Arguello to Morro Bay. Her best catch averaging 12 pounds (5.5 kg) was 140 albacore taken 200 miles west of Morro Bay in waters with sea-surface temperatures approximately 59°F (15.0°C). The Lusty left Ventura, California on July 5 and worked northward to Cape Flattery. The Lusty reported small catches near the Davidson Seamount and small, scattered catches off Point Arena and northward. Its best days of fishing were on July 11-12 when 41 and 59 albacore were caught from approximately 100-110 miles west of Point Arena. These fish averaged 12½-13 pounds (5.7-5.9 kg) and the sea-surface temperature was about 59°F (15.0°C). The third AFRF chartered jigboat, Four C's, left Astoria on July 13 and fished offshore to Cobb Seamount and off Newport, Oregon. The Four C's has caught only two albacore.

The Oregon Department of Fish and Wildlife also chartered a jigboat to scout the areas off Oregon during part of the first 2 weeks of July; however, no albacore were caught.

Catches made by San Diego based sportboats have ranged from less than one fish per passenger to better than three fish per passenger during the first 2 weeks of July. These boats generally fished from 60-90 miles south of San Diego, with the best catches in the second week of July being made in an area about 60 miles south of San Diego.

Sea-surface temperatures (SST) warmed from July 1-15 over the offshore areas of the eastern Pacific (see chart) at near-normal rates. Along the coast near Cape Blanco and east of 126°W, the 15-day warming trend was 1-2°F above normal and west of San Francisco between 124°W and 125°W, the SST's actually cooled 1-2° more than normal during the first half of July. The cooling of SST's west of San Francisco was associated with frequent periods of strong northerly winds and heavy mixing of colder, upwelled water from the coast. Near Cape Blanco the light winds and relative clear skies from July 1-15 resulted in more surface heating and less ocean mixing and upwelling than normal.

During the last half of July, based on the National Weather Service forecast of slightly above-normal surface pressures centered near 40°N, 140°W, it appears that off shore there will be a near-normal warming trend in SST's. However, south of Cape Mendocino and east of 125°W, SST's have been 1-2°F below normal during the past 15 days. It is expected that SST's will remain more than 1°F below normal in this area, especially within 100 miles of the coast where wind mixing and upwelling are expected to be most pronounced during the latter half of July. The areas with greatest warming of 1-2°F above normal will continue to be north of Cape Blanco from 50 to 200 miles off shore. This area is shown in the attached SST chart where the 56°F and 58°F isotherms bulge to the northeast.

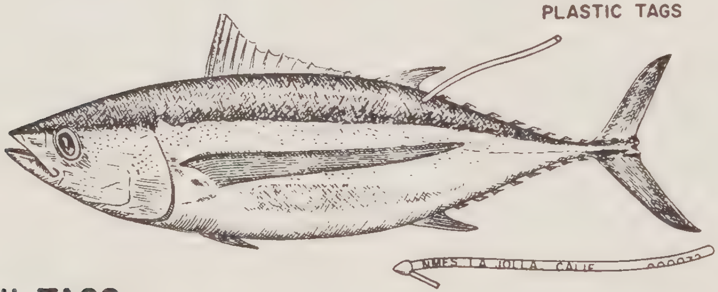
July 18, 1977

Staff, Albacore Fisheries Program
R. Michael Laurs, Leader

Figure 1a. Example of biweekly albacore Fish Bulletin.

$ REWARD $

FOR ALBACORE TUNA TAGS



YELLOW TAGS

THE NATIONAL MARINE FISHERIES SERVICE WILL PAY $ 2.00 FOR EACH YELLOW TAG RECOVERED. (NO NEED TO RETURN FISH)

RECORD:
- WHERE
- WHEN
- HOW

} *FISH WAS CAUGHT*

- LENGTH OF FISH (TIP OF LOWER JAW TO FORK OF TAIL)

FORWARD TO NMFS ADDRESS ON TAG

RED TAGS

THE NATIONAL MARINE FISHERIES SERVICE WILL PAY $ 50.00 FOR EACH RED TAG & FISH RETURNED. (FISH WITH TAG INTACT MUST BE RETURNED)

RECORD:
- WHERE
- WHEN
- HOW

} *FISH WAS CAUGHT*

- LENGTH OF FISH (TIP OF LOWER JAW TO FORK OF TAIL)

NOTIFY NMFS P.O. BOX 271, LA JOLLA, CA. TEL. (714) 453-2820

THE AMERICAN FISHERMEN'S RESEARCH FOUNDATION WILL AWARD CASH PRIZES FOR YELLOW & RED TAG NUMBERS DRAWN IN AN ANNUAL LOTTERY.

Figure 1b. Albacore tagging information included with biweekly Fish Bulletin.

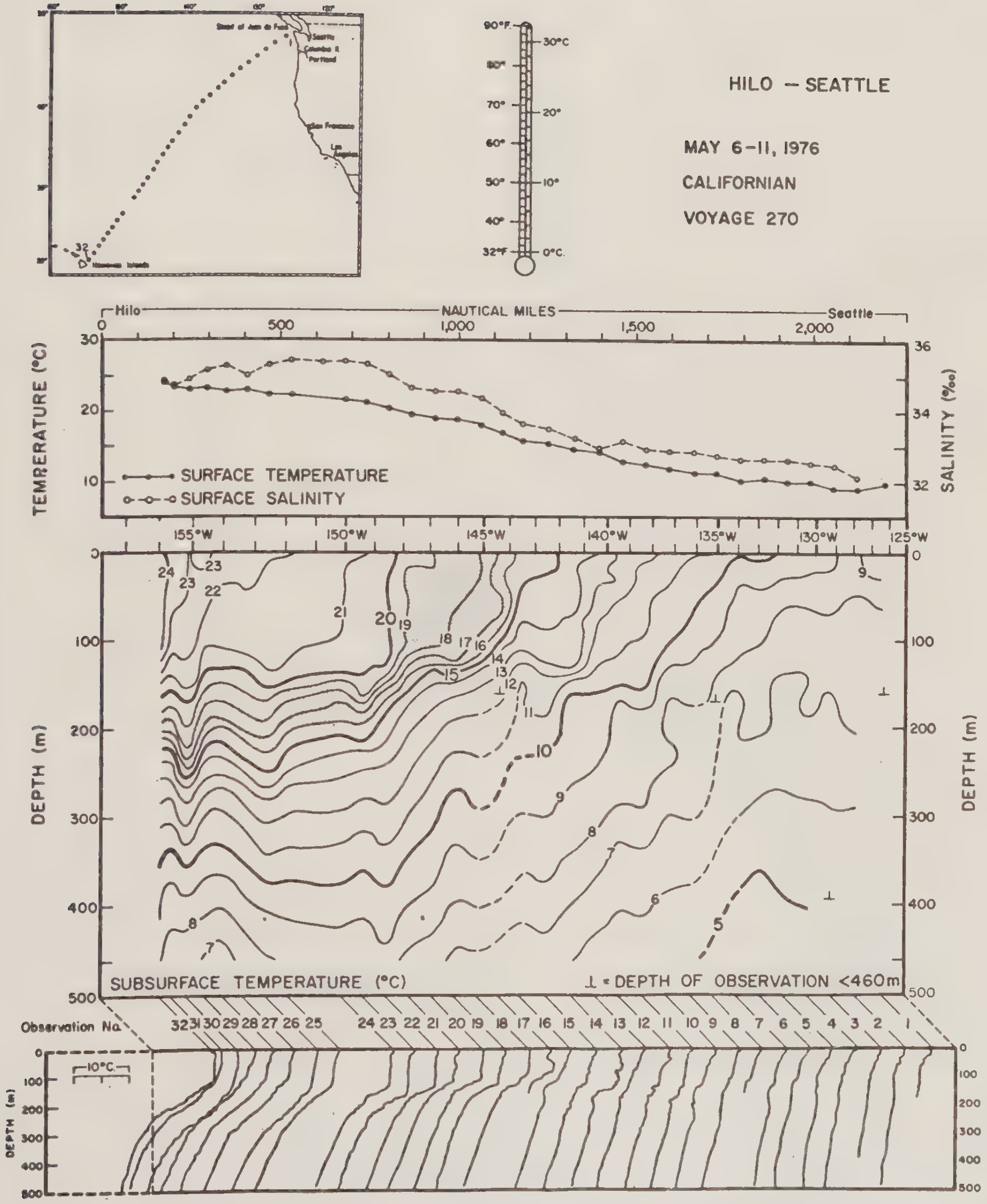


Figure 2a. Surface temperature and salinity and subsurface temperature structure from expendable bathythermograph observations between Seattle and Hawaii.

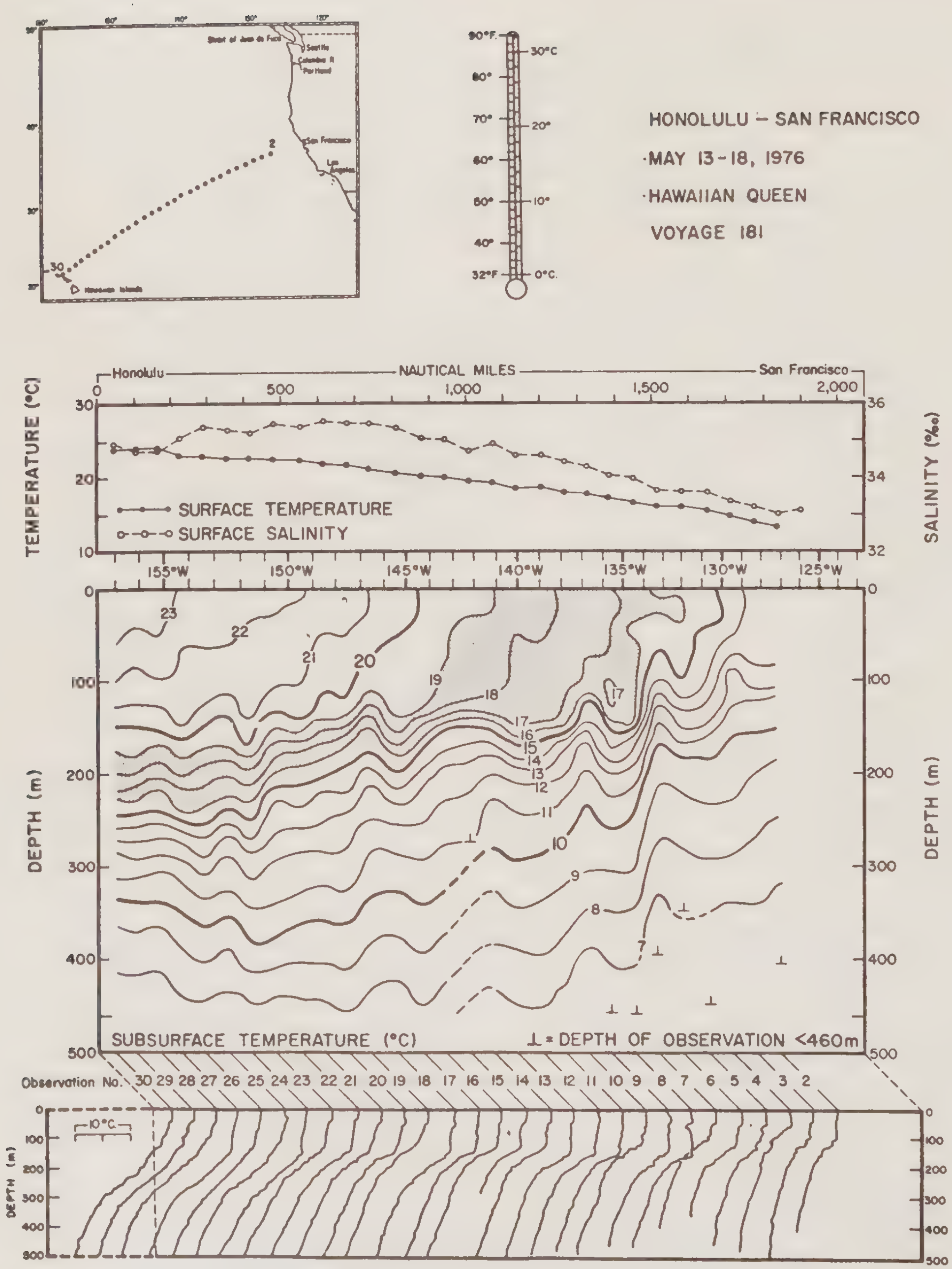


Figure 2b. Surface temperature and salinity and subsurface temperature structure from expendable bathythermograph observations between San Francisco and Hawaii.

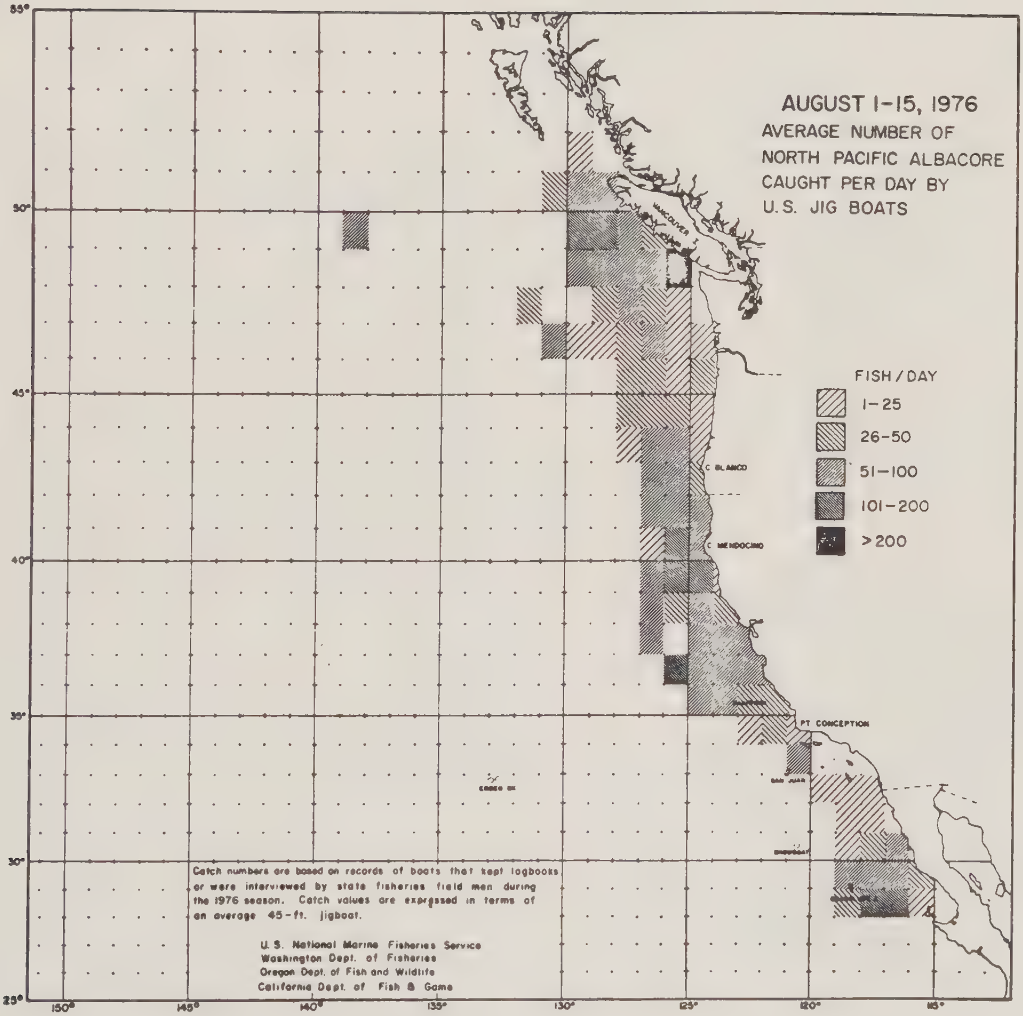
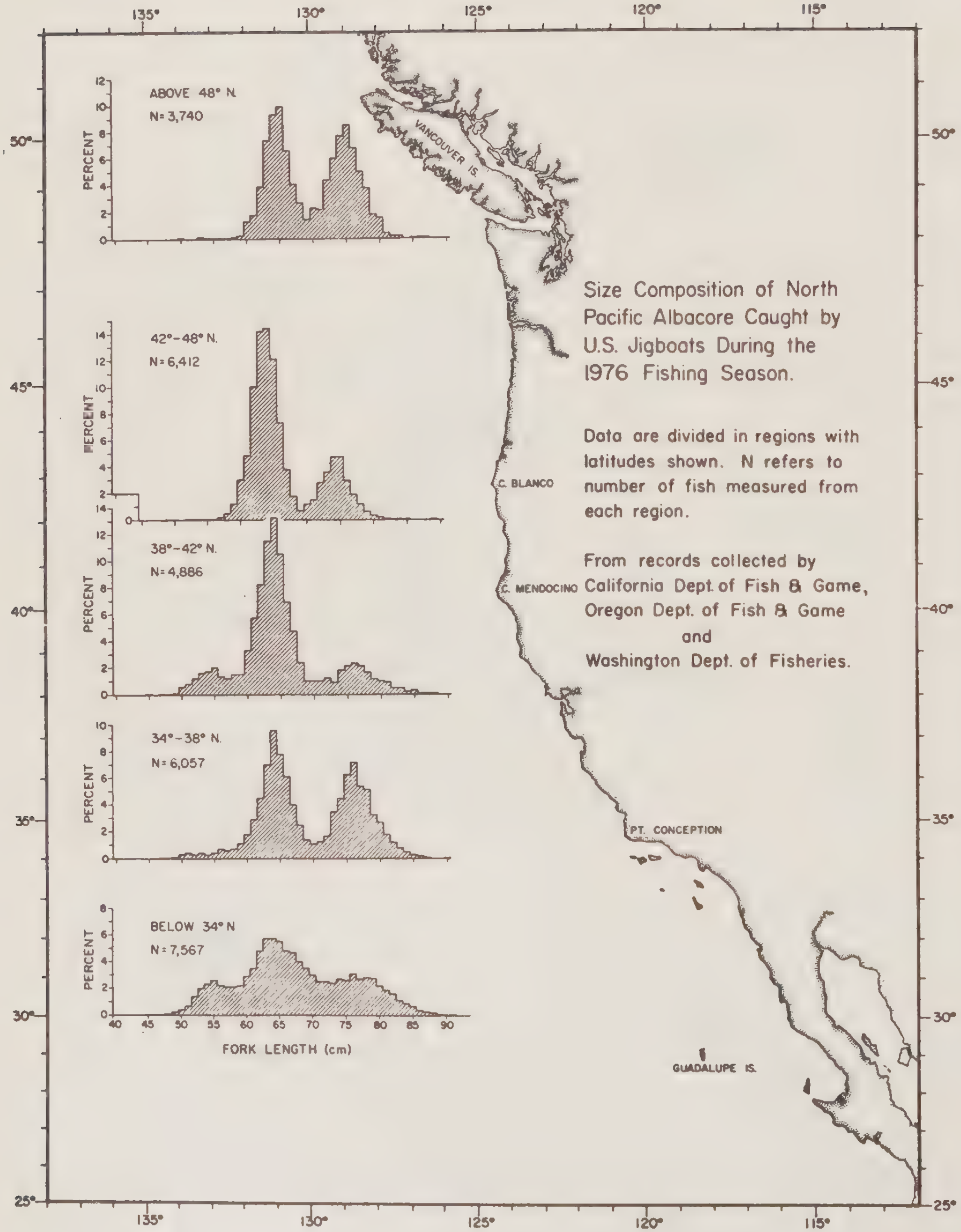

AUGUST 1-15, 1976
AVERAGE NUMBER OF
NORTH PACIFIC ALBACORE
CAUGHT PER DAY BY
U.S. JIG BOATS
FISH / DAY
▨ 1-25
▨ 26-50
▨ 51-100
▨ 101-200
■ >200
VANCOUVER I.
C BLANCO
C MENDOCINO
PT CONCEPTION
SAN JUAN
Catch numbers are based on records of boats that kept logbooks or were interviewed by state fisheries field men during the 1976 season. Catch values are expressed in terms of an average 45-ft. jigboat.
U. S. National Marine Fisheries Service
Washington Dept. of Fisheries
Oregon Dept. of Fish and Wildlife
California Dept. of Fish & Game
55°
50°
45°
40°
35°
30°
25°
150°
145°
140°
135°
130°
125°
120°
115°

Figure 3. Chart distributed to fishermen showing nominal catch per unit effort by 15-day period and 1° quadrangle.



Size Composition of North Pacific Albacore Caught by U.S. Jigboats During the 1976 Fishing Season.

Data are divided in regions with latitudes shown. N refers to number of fish measured from each region.

From records collected by California Dept. of Fish & Game, Oregon Dept. of Fish & Game and Washington Dept. of Fisheries.

135°
130°
125°
120°
115°
50°
45°
40°
35°
30°
25°
ABOVE 48° N.
N=3,740
42°-48° N.
N=6,412
38°-42° N.
N=4,886
34°-38° N.
N=6,057
BELOW 34° N
N=7,567
PERCENT
FORK LENGTH (cm)
40
45
50
55
60
65
70
75
80
85
90
VANCOUVER IS.
C. BLANCO
C. MENDOCINO
PT. CONCEPTION
GUADALUPE IS.

Figure 4. Chart distributed to fishermen showing size composition of albacore caught in commercial fishing.

7732

SMALL-SCALE MOVEMENTS OF ALBACORE, *THUNNUS ALALUNGA*, IN RELATION TO OCEAN FEATURES AS INDICATED BY ULTRASONIC TRACKING AND OCEANOGRAPHIC SAMPLING

R. Michael Laurs,[1] Heeny S. H. Yuen,[2] and James H. Johnson[3]

ABSTRACT

Studies with ultrasonic tracking techniques and oceanographic sampling demonstrated that oceanographic conditions play an important role in the local concentrations and movements of albacore, *Thunnus alalunga*, in U.S. coastal waters. Albacore show a tendency to congregate in the vicinity of coastal upwelling fronts, presumably to feed. They move away from the immediate area when upwelling ceases and the upwelling front is no longer present at the surface. The movements of albacore also appear to be related to the distribution of sea surface temperature, with fish spending little time in water with surface temperatures cooler than 15.0°C.

The average swimming speed for three fish tracked between 27.8 and 50 h was 1.6 knots (82.4 cm/s) with each fish exhibiting slightly faster swimming speeds during hours of daylight than during hours of darkness.

The albacore, *Thunnus alalunga* (Bonnaterre), is widely distributed in the Pacific Ocean. The single subpopulation which is found in the North Pacific (Otsu 1960) supports important surface commercial fisheries in coastal waters off North America and Japan and subsurface fisheries in the central temperate Pacific. The species is also highly prized by U.S. recreational fishermen. Passive tagging methods have been used to study large-scale migratory patterns of albacore in the North Pacific (Ganssle and Clemens 1953; Otsu 1960; Clemens 1961, 1963; Otsu and Uchida 1963; Laurs and Nishimoto[4]); however, information on small-scale movements is scant.

In order to examine the small-scale movements of schools of albacore and evaluate the effects that oceanographic conditions may have on the local concentrations and movements of albacore in coastal waters off the United States, studies were conducted with ultrasonic tracking techniques and oceanographic sampling.

Tracking the movements of animals to which ultrasonic transmitters have been attached is a technique that has been developed over the past two decades. This valuable technique has gained such wide application in recent studies of marine fishes and crustacea that it is more convenient to cite a bibliographic source (Stasko 1975) than to cite individual references.

METHODS

In the course of acoustic tracking studies, environmental data commonly have been collected for correlation with observed movements of the animal. At times, small auxiliary craft have been used for this purpose in support of the vessel doing the tracking, but usually the collection of environmental data has been done entirely from aboard the tracking vessel, necessarily limiting measurements to the ship's track. This study represents a significant expansion of supportive environmental data acquisition: for the first time a major oceanographic research vessel and an aircraft were coordinated with acoustic tracking of fish. The ultrasonic tracking experiment involved the use of the commercial albacore fishing baitboat *Linda* on charter to the American Fishermen's Research Foundation, the National Marine Fisheries Service (NMFS) RV *David Starr Jordan,* and a Coast Guard aircraft equipped with sea surface temperature measuring equipment.

Capture, Handling, and Tagging of Albacore

The capture of fish, tagging with ultrasonic

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[1] Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[2] Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 3830, Honolulu, HI 96812.

[3] Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 2725 Montlake Blvd. East, Seattle, WA 98112.

[4] Laurs, R. M., and R. N. Nishimoto. 1974. Joint NMFS-AFRF albacore tagging study. SWFC Admin. Rep. LJ-74-47:63-81.

Manuscript accepted October 1976.

transmitters, and tracking of the fish were done aboard *Linda* by three NMFS scientists with assistance from the crew of *Linda*. Albacore ranging in size from 74 to 87 cm fork length with estimated weights of 8.2 to 13.6 kg were caught on hook and line baited with anchovy. The fish was played an average of 5 min before being brought on board by dip net. Without removing it from the net, the fish to be tagged was placed on its side on a plastic covered foam measuring pad on the deck where it was measured to the nearest lower centimeter and the transmitter was attached. A wet burlap bag was placed over its head to keep the fish calm. No anesthetic was used.

The ultrasonic transmitter was attached to the back of the fish, immediately in front of the second dorsal fin, with two sutures through the skin and muscle tissue in that area. Upon completion of tagging, fish were immediately replaced in the water. Total elapsed time for fish out of water was between 1 and 1½ min. Within 2 to 4 s after being released, each tagged fish was observed righting itself and actively swimming downward and out of sight. One fish was tracked at a time. The three fish tracked longer than 24 h were tagged in the manner described above. Several fish tracked for shorter periods early in the cruise were tagged by inserting the transmitter into the stomach through the mouth. This latter method was abandoned when it appeared that acoustic signal attenuation caused by internal implacement was resulting in an inadequate receiving range.

Tracking Equipment

The transmitter tags and hydrophone used were built by the Northwest and Alaska Fisheries Center, Seattle, Wash. The tags were cylindrical measuring 8.2 by 1.9 cm, weighing 67 g in air and 43 g in water, and emitted a 45 or 50 kHz signal at a pulse rate of 120 pulses/min. Acoustic source level of the tag was 63 dB (reference to 1 μbar at 1 m in fresh water).

The hydrophone was a tuned 6-element array (sensitivity - 69 dB, reference to 1 μbar at 1 m) with a beam width of 20° horizontally and 40° vertically at the 3-dB point. This was attached to the lower end of a 3-cm aluminum pipe, bracketed to the starboard rail amidship of the tracking vessel. A geared electric motor at the top of the pipe rotated the hydrophone, which was remotely controlled from the tracking station in the wheelhouse. Signals picked up by the hydrophone were fed into a Lawson VLF-1[5] superheterodyne receiver.

Tracking Procedure

With the hydrophone remote-control unit installed in the pilothouse of *Linda* alongside the engine and steering controls and the receiver placed about 2 m away, one person was able to operate the tracking system and control the vessel simultaneously. Directing the hydrophone for maximum signal, the operator moved the vessel on that heading until satisfied, on a basis of signal strength, with his proximity to the fish. The receiving range varied widely according to sea state, but on the average *Linda* was kept an estimated 500 m from the tagged fish. The fish moved continuously and so, consequently, did the vessel, but vessel speed of more than 2 knots was seldom necessary to keep up with the fish. Position of the tracking vessel was determined approximately once an hour and was taken also to represent the position of the fish at that time. Most of the navigation for *Linda* was done by the nearby *David Starr Jordan*, with a combination of Loran, radar, and Omega systems.

Oceanographic Observations Made From Ship

Detailed oceanographic observations were made aboard *David Starr Jordan* in support of the ultrasonic tracking experiments. These included continuous monitoring of surface temperature and salinity and measurements of subsurface temperature and salinity at selected stations. Observations were also made to evaluate biological factors of the marine environment. These included continuous monitoring at the surface and subsurface measurements at selected stations of chlorophyll a by fluorometric techniques (Holm-Hansen et al. 1965), measurements of primary productivity by ^{14}C methods (Owen and Zeitzschel 1970), and estimates of the standing stocks of potential albacore food organisms.

The estimates of potential albacore forage were derived from hauls made with a 1.8-m Isaacs-Kidd midwater trawl (IKMT) lined with a 58-mm mesh. The hauls were taken during hours of darkness from the surface to a depth of approximately 175 m at a ship speed of about 5 knots. The volumes of water strained were estimated from data obtained by a TSK[6] depth-distance recorder mounted in the mouth of the trawl. The Formalin-preserved IKMT catches were sorted into several categories of fishes, cephalopods, crustaceans, and other animals, and the displacement volume of each of these kinds of animals was measured and standardized in ml/1,000 m³ of water filtered for each haul. The standardized values of 1) larval and juvenile fishes, 2) epipelagic fishes, 3) cephalopods, and 4) crustaceans were summed for each haul and collectively regarded as potential albacore forage. Analysis of stomach contents of albacore has shown that these categories of organisms are important in the diet of albacore (Pinkas et al. 1971) in this area.

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[5] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Oceanographic Observations Made by Aircraft

A Coast Guard aircraft equipped with a Barnes PRT-5 infrared radiometer made measurements of sea surface temperature for evaluation of the small-scale features and changes in the distribution of sea surface temperature.

RESULTS AND DISCUSSION

Six albacore were tagged and tracked with ultrasonic equipment for periods ranging from about 2 to 50 h and distances ranging from 6.5 to 150.7 km (3.5 to 81.3 nmi). Results will be presented for fish numbers 4, 5, and 6, which were tracked for 27.8, 41.4, and 50.0 h, respectively. There are too few data for discussion for fish numbers 1, 2, and 3 because of the short periods that the fish were tracked. A summary of the tracking date and time, tagging location, distance tracked, and fork length of fish for fish numbers 4, 5, and 6 is given in Table 1.

Tagged fish rejoined untagged albacore after being returned to the water, and tended to remain in their company. Surface "boils" characteristic of albacore were frequently sighted close by *Linda*, and approximately 30 fish of the same general size as fish tagged with ultrasonic transmitters were caught by the crew while tracking was in progress. Also, one tagged fish "lost" the previous day was heard intermittently over a 4-h period during the track that followed. We were able to distinguish between the two fish because of slightly different signals from the tags.

TABLE 1.—Summary of tracking date and time, fork length of albacore, location of tagging, and distance tracked.

No.	Date	Time	Fork length	Tagging location Lat.	Tagging location Long.	Distance
4	8-16-72 to 8-17-72	1445 to 1845	84 cm	36°49.8′N,	122°19.1′W	41.6 nmi (77.1 km)
5	8-19-72 to 8-20-72	0715 to 2345	87 cm	36°50.3′N,	122°13.6′W	61.4 nmi (113.8 km)
6	8-25-72 to 8-27-72	1000 to 1205	85 cm	35°20.0′N,	121°22.0′W	81.3 nmi (150.7 km)

Speed of Albacore Movements

Swimming speeds for albacore were estimated from straight-line calculations using position of the tracking vessel. The average swimming speed, based on the total distance and time that the fish were tracked, for fish numbers 4, 5, and 6 was about 1.6 knots (82 cm/s). Speeds calculated from hourly ship positions for each fish ranged from 0.1 to 3.6 knots (5 to 185 cm/s). Table 2 shows the percentage of time each fish spent at various swimming speeds. There were day-night differences in the rate of movement, with fish exhibiting faster swimming speeds during hours of daylight (0500 to 1900 h) than during hours of darkness. The average speed during daylight for fish numbers 4 and 5 was 1.7 knots (88 cm/s) and for number 6 was 2.1 knots (108 cm/s). The average speed during nighttime for fish numbers 4 and 6 was 1.3 knots (67 cm/s) and for fish number 5 was 1.0 knot (51 cm/s). Table 3 gives a summary of time, distance, and mean speeds.

Moonlight also appeared to influence the rate of movement of fish number 5. This fish, which had been moving steadily at about 2.0 knots (103 cm/s) for about 3 h after moonrise and following a course about 20° west of the full moon, came to a near stop

TABLE 2.—Percent of time each albacore spent at various swimming speeds.

Speed knots	Speed cm/sec	Fish no. 4	Fish no. 5	Fish no. 6
		Percent		
<0.5	<26	8.0	5.9	0.0
0.5-0.9	26- 46	12.0	23.5	15.8
1.0-1.4	51- 72	32.0	35.3	28.9
1.5-1.9	77- 98	24.0	11.8	15.8
2.0-2.4	103-124	16.0	17.6	28.9
2.5-2.9	129-149	4.0	2.9	0.0
3.0-3.4	154-175	0.0	2.9	10.5
>3.5	>175	4.0	0.0	0.0

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[6] Tsurumi Seiki Kosakusho Co., Ltd., Yokohama, Japan.

TABLE 3.—Summary of duration and distance tracked and mean speed of albacore tracked with ultrasonic transmitters.

Item	Fish no. 4	Fish no. 5	Fish no. 6
Time tracked (h)	27.8	41.4	50.0
Distance tracked:			
nmi	41.6	61.4	81.3
km	77.1	113.8	150.7
Mean speed:			
knots	1.6	1.5	1.6
cm/s	82	77	82
bl/s[1]	0.98	0.88	0.96
Mean speed, day:[2]			
knots	1.7	1.7	2.1
cm/s	88	88	108
bl/s[1]	1.05	1.01	1.27
Mean speed, night:[3]			
knots	1.3	1.0	1.3
cm/s	67	51	67
bl/s[1]	0.80	0.59	0.79

[1] bl/s = body lengths per second
[2] 0500-1900 h.
[3] 1900-0500 h.

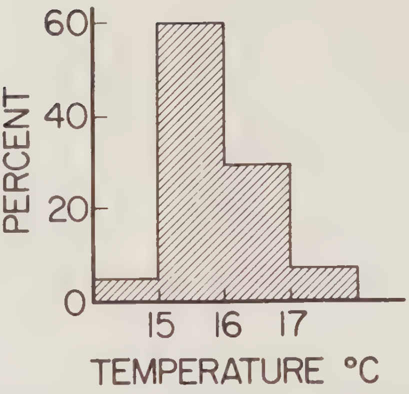


FIGURE 1.—Percent of time (hours) spent in waters of various sea surface temperature by albacore numbers 4, 5, and 6.

for nearly an hour when the moon was suddenly obscured by dense fog at about 0300 h.

The mean swimming speeds calculated from the tracking experiment are close to estimates of swimming speed derived from passive tagging results. For example, based on data given in the Japanese Fisheries Agency (1975) report, two tagged albacore, which were released in the western North Pacific and recovered in the eastern North Pacific about 3½ mo later, traveled at 1.1 knots (57 cm/s), assuming they followed a great circle route and were caught the day they arrived at the recovery location. The mean swimming speeds found in this study are slightly less than twice the calculated minimum swimming speed necessary for an 80-cm albacore to maintain hydrostatic equilibrium (Dotson 1977).

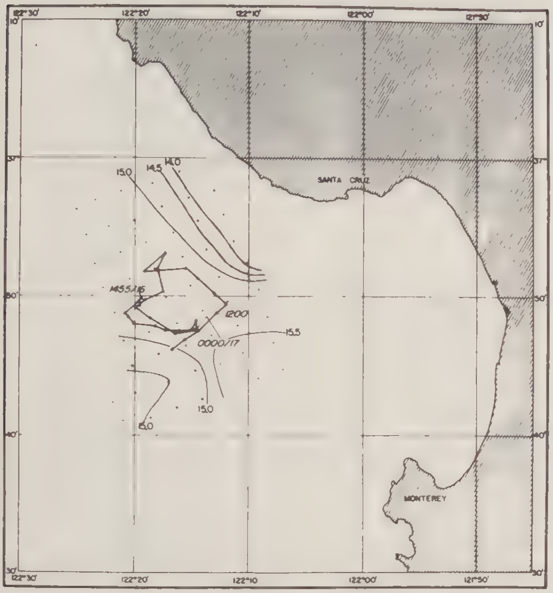
Relationship of Albacore Movements to Sea Surface Temperature

The movements of the fish tagged with ultrasonic transmitters appeared to be influenced by the distribution of sea surface temperature. Figure 1 shows the percentage of the time that fish numbers 4, 5, and 6 spent in waters of various surface temperatures. Fish number 6 spent no time in water with surface temperatures less than 15.0°C although roughly 20% of the waters 5 nmi distant on both sides of the path followed by the fish were colder than 15.0°C. Fish number 4 was in water which had surface temperatures colder than 15.0°C 12.5% of the time, while 35% of the waters 5 nmi distant on both sides of the path followed by the fish was colder than 15.0°C. Fish number 6 was in water with surface temperatures warmer than 17.0°C 22% of the time, which coincided with the percentage of area with temperatures greater than 17.0°C. Water with temperature higher than 17.0°C was not available to fish numbers 4 and 5.

These results indicate that the transmitter-tagged fish spent very little time in water with surface temperatures less than 15.0°C. This is especially evident when charts showing the tracks followed by the fish and the contoured field of sea surface temperature observed by *David Starr Jordan* at the time of tracking are examined. Figures 2, 3, and 4 show tracks followed by fish numbers 4, 5, and 6, respectively, and sea surface temperature. In these figures, temperatures less than 15.0°C, which are considered below the habitat preference for albacore (Clemens 1961), are shaded. Fish number 4 remained in the vicinity of a band of water cooler than 15.0°C for nearly the total time it was tracked, but did not appear to enter it (Figure 2). Fish number 6 traveled on a southerly course, in a corridor of warm water which was sandwiched between two wedges of cool water on 25 August, but did not enter the cool water on either side except very briefly at the start of tracking (Figure 4). When the fish passed to the south of the cool water, where there was a large area of water warmer than 15.0°C, the fish changed its direction generally to a more southwesterly course.

Relationship of Albacore Movements to Upwelling Temperature Fronts

A well-developed temperature front occurs at the boundary between cool, biologically rich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SANTA CRUZ
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1455/16
1200
0000/17
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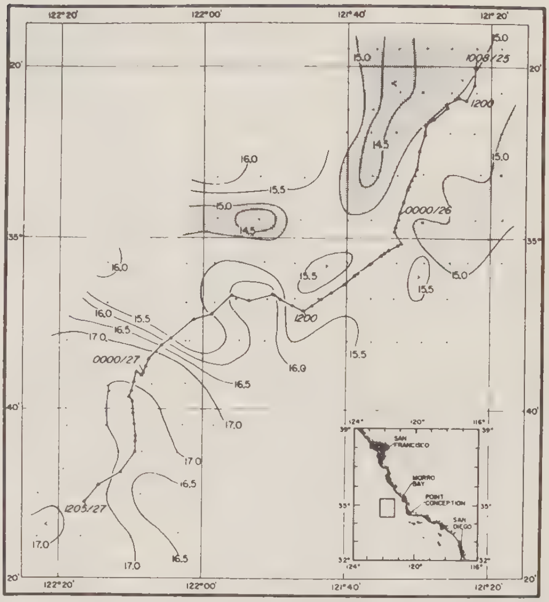
15.0
15.0

FIGURE 2.—Movements of albacore number 4 as indicated by ultrasonic tracking and contoured field of sea surface temperature in degrees Celsius. Triangles on fish track indicate hourly position. The time and date that tracking commenced is noted at the starting location and shown above and below a slash mark, respectively. The 0000 and 1200 h local time positions are also indicated. Dots show where temperature observations were made by *David Starr Jordan*. Temperatures below 15.0°C are shaded.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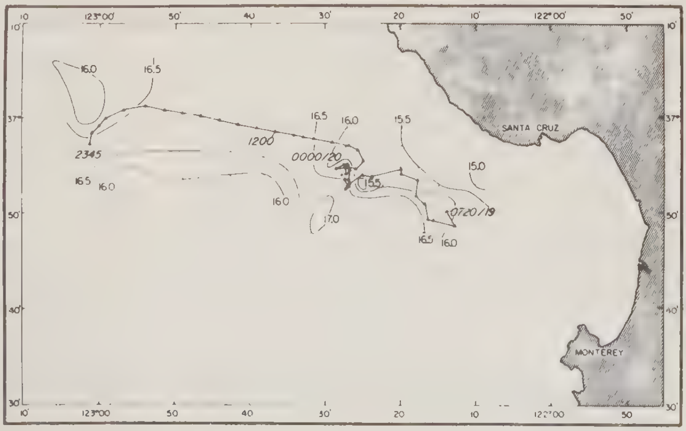
0000/27
1203/27
SAN FRANCISCO
MORRO BAY
POINT CONCEPTION
SAN DIEGO
124°
120°
116°
39°
35°
32°

FIGURE 4.—Movements of albacore number 6 as indicated by ultrasonic tracking and contoured field of sea surface temperature in degrees Celsius. Triangles on fish track indicate hourly position. The time and date that tracking commenced is noted at the starting location and shown above and below a slash mark, respectively. The 0000 and 1200 h local time positions are also indicated. Dots show where temperature observations were made by *David Starr Jordan*. Temperatures below 15.0°C are shaded.

upwelled water and warmer, nonupwelled water (Smith 1968). The effects that an upwelling front may have on the movements of albacore were indicated during the ultrasonic tagging experiment. On 17 August, during tracking operations for fish number 4, a relatively well-developed upwelling surface temperature front was observed in the northeast portion of the tracking area. The upwelling was caused by brisk northerly winds which had been blowing for several days. The remainder of the area surveyed has a rather simple surface temperature distribution mostly within the temperature range considered as the habitat preference for albacore (Figure 2).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15.5
15.0
17.0
SANTA CRUZ
MONTEREY

FIGURE 3.—Movements of albacore number 5 as indicated by ultrasonic tracking and contoured field of sea surface temperature in degrees Celsius. Triangles on fish track indicate hourly position. The time and date that tracking commenced is noted at the starting location and shown above and below a slash mark, respectively. The 0000 and 1200 h local time positions are also indicated. Dots show where temperature observations were made by *David Starr Jordan*.

Infrared radiation temperature measurements made during an overflight by the Coast Guard aircraft on 16 August showed that the water on the cold side of the front continued to decrease toward shore to values below 13.0°C.

Fish number 4 traveled in about an 8 × 8 nmi area on the warm side of the upwelling front and in close proximity to it for nearly the total time the fish was tracked. Subsequently, high winds and rough seas made tracking difficult and the signal from the fish was lost during hour 27 of tracking.

Fish number 5 exhibited a much different pattern of movement than did number 4 (compare Figures 2 and 3). It moved many miles from the location where it had been tagged, in a general northwesterly direction, rather than remaining in the local vicinity as fish number 4 had done.

Examination of oceanograhic data revealed that marked changes in the distribution of sea surface temperature had occurred between 17 and 19 August (compare Figures 2 and 3). Upwelling had subsided, the upwelling temperature front was no longer present on 19 August, and the temperature over much of the area had increased by about 1.5°C. The breakdown of the upwelling front and warming was due to a slackening and shifting of the winds to a westerly-southwesterly direction which allowed a thin layer of warmer offshore water to flow toward the coast.

It is presumed that the school of fish with which fish number 4 was traveling remained in the vicinity of the upwelling front to feed in the highly productive water associated with the upwelling. Measurements of chlorophyll were high in the tracking area and showed a very strong positive gradient on the cold side of the upwelling front (Figure 5). Measurements of ^{14}C uptake indicated a primary production rate integrated over the euphotic zone (0 to 36 m) of 1,511 mg C/m² per day. The biomass of potential albacore food organisms was also high, ranging from about 20 to 56 ml/1,000 m³ water strained, in midwater trawl collections made at night in the nearby area where tracking took place (Table 4).

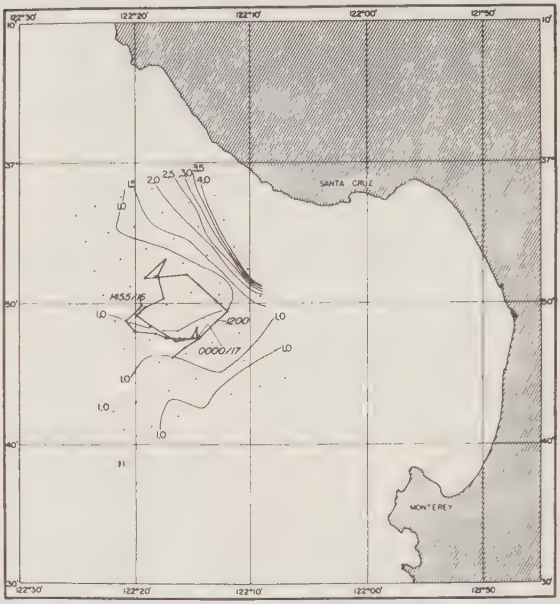

FIGURE 5.—Movements of albacore number 4 as indicated by ultrasonic tracking and the distribution of surface chlorophyll in milligrams per cubic meter.

TABLE 4.—Summary of dates, times, positions, and estimates of potential albacore forage, 1972.

Fish no.	IKMT no.	Date	Time	Lat. (N)	Long. (W)	Forage biomass (ml/1,000 m³)
4	1	15 Aug.	2200-2240	36°50′	122°14′	28.8
	2	16 Aug.	2159-2238	36°47′	122°15′	36.2
	3	17 Aug.	2137-2215	36°55′	122°24′	56.2
	4	18 Aug.	0032-0111	36°53′	122°16′	51.5
	5	18 Aug.	0130-0210	36°52′	122°19′	30.4
	6	18 Aug.	0232-0311	36°49′	122°22′	37.7
	7	18 Aug.	0352-0430	36°50′	122°11′	30.7
	8	18 Aug.	0516-0553	36°41′	122°19′	29.8
5	9	21 Aug.	2116-2150	37°06′	122°50′	5.7
	10	21 Aug.	2236-2314	36°57′	122°59°	10.1
	11	22 Aug.	0032-0115	36°54′	122°38′	24.5
	12	22 Aug.	0152-0231	36°48′	122°30′	23.1
	13	22 Aug.	0302-0341	36°55′	122°25′	10.6
	14	22 Aug.	0412-0450	36°52′	122°17′	24.9
6	15	27 Aug.	2119-2156	34°40′	122°14′	5.8
	16	27 Aug.	2241-2320	34°48°	122°02′	8.0
	17	28 Aug.	0040-0122	34°53′	121°51′	5.9
	18	28 Aug.	0214-0251	35°07′	121°29′	10.1
	19	28 Aug.	0325-0402	35°15′	121°26′	19.6

Albacore were frequently seen boiling in the area nearby the upwelling front by personnel aboard *Linda* and *David Starr Jordan*. Also, observers aboard the Coast Guard aircraft noted about 25 to 30 commercial albacore jig boats fishing immediately on the warm side of the front in water warmer than 15.0°C. High biological production in the area of the upwelling front was also indicated by large numbers of sea birds and numerous sightings of marine mammals, including blue whales and other whales.

It is possible that fish number 5 and the school it was traveling with left the immediate area where it had been tagged because food organisms were no longer concentrated there due to the breakdown of the upwelling front. This explanation is supported by the observation on 19 August of an overall reduction in the concentration of surface

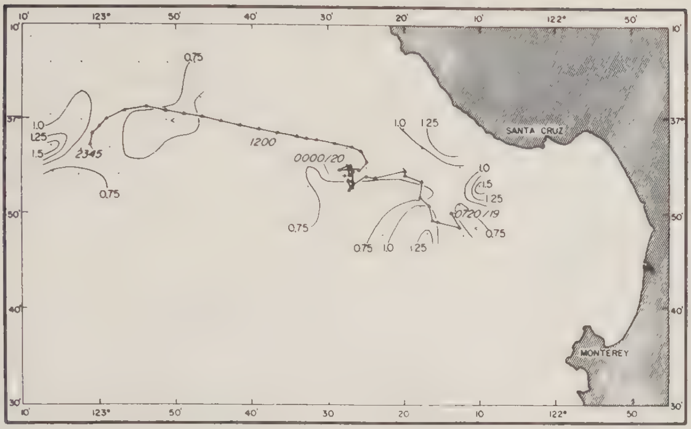

FIGURE 6.—Movements of albacore number 5 as indicated by ultrasonic tracking and the distribution of surface chlorophyll in milligrams per cubic meter.

chlorophyll a, as much as three to four times lower in waters where upwelling had been taking place on 17 August (Figure 6). Also, measurements of ^{14}C uptake indicate that the rate of primary production was about 33% lower, 1,014 mg C/m^2 per day, than it had been when fish number 4 was tracked. In addition, estimates of biomass of potential albacore forage organisms taken in midwater trawl hauls made during tracking operations for fish number 5 were less, ranging from about 6 to 25 ml/1,000 m^3 of water filtered (Table 4), than during tracking operations for fish number 4. (Relatively low chlorophyll a values (Figure 7) and albacore forage biomass values (Table 4) were also observed during tracking operations for fish number 6.)

While tracking information on only two fish does not provide sufficient data from which to make generalizations, the results suggest that 1) albacore concentrate in the vicinity of upwelling fronts, presumably to feed, and 2) albacore move away from the immediate area when upwelling ceases and the upwelling front is no longer present at the surface. Pearcy and Keene (1974) discussed the possibility of albacore congregating in the region of upwelling fronts. The concentration of albacore in the vicinity of upwelling fronts has also been indicated by high catch rates made by fishing and research vessels near upwelling fronts (Pearcy and Mueller 1970; Panshin 1971; Laurs 1973).

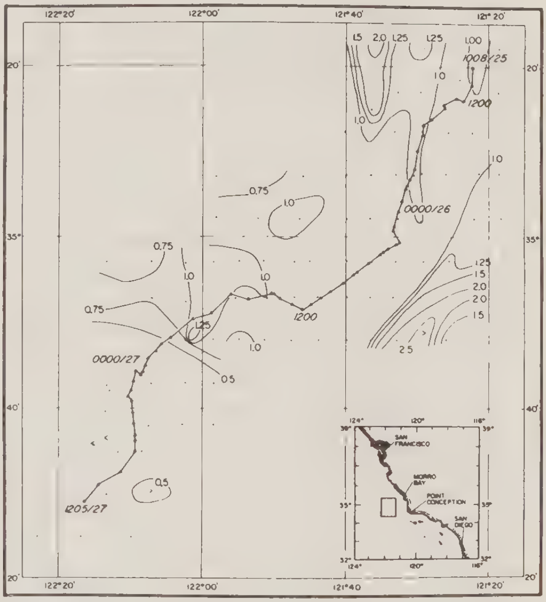

FIGURE 7.—Movements of albacore number 6 as indicated by ultrasonic tracking and the distribution of surface chlorophyll in milligrams per cubic meter.

Relationship of Albacore Movements to Other Sea Surface Temperature Fronts

During the tracking operations, it appeared that fish numbers 5 and 6 tended to slow down when crossing temperature fronts where the temperatures on both sides of the front were within the favorable range for albacore. To examine this more closely, mean speeds were estimated for tagged fish when they were within a 5-nmi distance before crossing and after crossing the temperature front and when crossing the front. A sea surface temperature front was defined as a change in surface temperature of 0.5°C or larger in a nautical mile (0.003°C/m). The results are summarized in Table 5 and show that for the three cases examined, 1) the mean speed was slower when crossing the front than it was before

TABLE 5.—Mean speed crossing temperature front[1] and mean speed within 5-nmi radius before and after.

Item	Fish no.	Date	Time	Total (h)	Total distance		Mean speed	
					(nmi)	(km)	(knots)	(cm/s)
Before	5	8/19	1330-1600	2.5	5.0	9.3	2.0	103
At front	5	8/19-20	1600-0300	11.0	7.8	14.4	0.7	36
After	5	8/20	0300-0800	5.0	7.0	13.0	1.4	72
Before	6	8/26	1700-1900	2.0	5.6	10.4	2.8	144
At front	6	8/26	1900-2100	2.0	3.7	6.9	1.8	93
After	6	8/26-27	2100-0200	5.0	8.0	14.8	1.6	83
Before	6	8/26	0800-1230	4.5	6.1	11.3	1.4	72
At front	6	8/26	1230-1400	1.5	2.0	3.7	0.7	36
After	6	8/26	1400-1600	2.0	5.2	9.7	2.6	134

[1] $\Delta T \geq 0.5°C/1.0$ nmi.

crossing the front in all three cases, and 2) the mean speed was slower when crossing the front than after crossing the front in two cases. These data should be viewed with caution, however, because in two instances, daytime and nighttime data were used together and some of the differences in speed may be due to variation associated with time of day. The relationship did hold up well in the single case when daytime data only were used.

We think the changes in swimming behavior observed at temperature fronts reflected perception and response to the increased temperature gradient per se. In the case of the alteration in the swimming pattern of fish number 5 as it encountered a temperature front at lat. 36°53′N, long. 122°27′W (Figure 3), there was no sharp gradient in any of the other environmental parameters we measured.

That tunas can perceive abrupt temperature changes as small as 0.1°C has been demonstrated by Steffel et al. (1976) for captive kawakawa, *Euthynnus affinis*. Moreover, a mechanism has recently been suggested (Neill et al. in press) whereby tunas might be able to orient themselves in temperature gradients much gentler than those of our fronts, perhaps even as slight as 0.0001°C/m; this speculative mechanism invokes the large thermal inertia of tunas as a device for thermal "memory."

Movements of Albacore in Relation to Vertical Thermal Structure

The availability of albacore in offshore waters has been shown to be related to vertical thermal structure (Laurs and Lynn[7]). However, no obvious relationship was observed in this study between the movements of sonic-tagged albacore in coastal waters and subsurface temperature structure. This may be due to the complicated vertical temperature structure that was observed in the areas where fish were tracked and the lack of data on the depth of the fish.

SUMMARY

Six albacore were tagged and tracked with ultrasonic equipment for periods ranging from 2 to 50 h and distances ranging from 6.5 to 150.7 km (3.5 to 81.3 nmi). The average swimming speed for these fish tracked between 27.8 and 50.0 h was 1.6 knots (82 cm/s) with each fish exhibiting slightly faster swimming speeds during the day than during the night. The mean swimming speeds observed during the tracking experiment are similar to estimates of swimming speed derived from passive tagging results and about twice the calculated minimum swimming speed necessary to maintain hydrostatic equilibrium.

The tracking experiment indicated that oceanographic conditions may play an important role in the local concentrations and movements of albacore in coastal waters. The movements of fish appeared to be related to the distribution of sea surface temperature, with transmitter-tagged fish spending very little time in water with surface temperatures less than 15.0°C. The results also indicate that upwelling temperature fronts may markedly influence the local concentration of albacore, with albacore tending to concentrate in the vicinity of upwelling fronts, presumably to feed, and moving away from the immediate area when upwelling ceases and the upwelling front is no longer present at the surface. There was also some indication that albacore tended to slow down when crossing sea surface temperature fronts where the temperatures on both sides of the front were within the optimal range for albacore.

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Finally, the tracking experiment demonstrated that acoustic tracking of albacore is feasible and that it can be a useful tool in studies designed to understand better the relationships between albacore and the marine environment.

ACKNOWLEDGMENTS

We acknowledge the assistance provided in the tracking operations by Michael Swiston, and Scotty Hazelton and crew of *Linda*, the U.S. Coast Guard, Pacific Area, for providing aircraft overflights, and James Squire for assistance in making and processing the airborne radiometer temperature observations. We thank Charles Forster and crew of the RV *David Starr Jordan* for the cooperative support in making oceanographic observations, and the American Fishermen's Research Foundation for providing funds for the charter of *Linda*. We also thank M. Blackburn, J. J. Magnuson, W. H. Neill, and W. G. Pearcy for critically reviewing the manuscript.

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MATURATION AND INDUCED SPAWNING OF CAPTIVE PACIFIC MACKEREL, *SCOMBER JAPONICUS*

Roderick Leong[1]

ABSTRACT

Pacific mackerel, *Scomber japonicus*, became sexually mature under laboratory conditions and were induced to spawn with hormone injections. Fish caught before the major spawning season became mature under the natural photoperiod and under artificial photoperiods of 4 h light 20 h dark, 8 h light 16 h dark, and 16 h light 8 h dark. Mackerel caught near the end of the spawning season redeveloped their gonads more rapidly at 18°C than at 15°C or ambient temperature. A 16°C-14 h light 10 h dark environment was effective in maintaining mackerel in spawning condition beyond the normal spawning season. Any of three combinations of hormones induced spawning: gonadotropin from ground salmon pituitary followed 24 h later by gonadotropin from pregnant mare serum; human chorionic gonadotropin followed 24 h later by gonadotropin from pregnant mare serum; and salmon pituitary plus human chorionic gonadotropin followed 24 h later by salmon pituitary plus human chorionic gonadotropin plus gonadotropin from pregnant mare serum. The hormones did not induce spawning when used individually. A procedure for routine spawning of Pacific mackerel is described.

Laboratory studies of the biology of pelagic fish larvae are often limited by the uncertainty of collecting eggs at sea. An alternative to collecting eggs at sea is the maturation and spawning of fish in the laboratory. This objective was met for the northern anchovy, *Engraulis mordax* (Leong 1971). Another species whose larvae are under study at the Southwest Fisheries Center is the Pacific mackerel, *Scomber japonicus* Houttuyn, but the eggs are not available off the southern California coast during most of the year. To increase the availability of mackerel eggs for experimental work, I began a study designed to develop procedures for routinely spawning mackerel on demand throughout the year. My approach was to first find a suitable photoperiod-temperature environment which would encourage maturation and to subsequently induce spawning with gonadotropic agents. This report contains observations on the maturation of mackerel under different photoperiod-temperature conditions in the laboratory; results of exploratory tests with hormones to induce spawning; and a description of a procedure currently used to spawn mackerel.

I followed the maturation of mackerel under four photoperiods (4 h light 20 h dark, 8L16D, 16L8D, and ambient day length) and three temperatures (15°C, 18°C, and ambient 12.8° to 19°C). I also examined the effectiveness of a 16°C-14L10D environment for maintaining mackerel in spawning condition after the normal spawning season. The hormones tested for the induction of spawning were gonadotropin from ground salmon pituitary, human chorionic gonadotropin, and gonadotropin from pregnant mare serum. The importance of the photoperiod-temperature environment in regulating maturation in fish and the use of gonadotropins for inducing spawning are well known from the early review of Pickford and Atz (1957), but observations on marine pelagic species are still limited. These are the first observations on the maturation and spawning of a scombrid fish under laboratory conditions.

METHODS

Maturation of Mackerel Under Four Photoperiods

Knaggs and Parrish (1973) examined the ovaries of mackerel from the commercial catch and concluded that *S. japonicus* can spawn from March through October but that the majority spawn from April through August. Kramer (1960), using sea-caught larvae as criteria, concluded that spawning occurs from late April or early May to August.

The fish used in these experiments were caught off the southern California coast by hook and line

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Manuscript accepted September 1976
FISHERY BULLETIN: VOL. 75, NO. 1, 1977

between 1 February and 7 March 1973. The dates of capture were 1 to 2 mo in advance of the major spawning season. The fish ranged from 325 to 340 mm fork length; most fish of this size are capable of spawning (Knaggs and Parrish 1973). During the period of collection, the fish were held under continuous incandescent lighting and a temperature of 19°C. These were arbitrary holding conditions.

On 14 March, 1 wk after the last fish was captured, the mackerel were divided into four groups and placed in three indoor plastic swimming pools (4.6 m in diameter, 1 m water depth) and one outdoor pool (7.3 m in diameter, 1 m water depth). Each of the three indoor pools was enclosed in a separate room lined with black opaque polyethylene film. A 200-W incandescent bulb, 1.2 m above the water surface, illuminated each indoor pool during the artificial day. A timer-controlled rheostat gradually lit and dimmed the bulb over 30 min to avoid startling the fish. The length of day was considered as the time of full illumination. Two 3-W lamps, 1 m above the water surface, burned continuously and provided low-level illumination during the dark period. The light intensity was about 215 lx at the brightest spot on the surface during the day and less than 5.4 lx at night. The outdoor pool was shielded from direct sunlight by an opaque plastic canopy 1.2 m above the water surface but the sides were open and the fish received a natural photoperiod.

Temperature control was achieved with a commercial temperature regulator and mixing valve unit which automatically adjusted the inflow of chilled (10°C) and heated (20°C) seawater to maintain a desired pool temperature. For this series of observations the temperature was set at 19° ± 0.5°C for all tanks. I chose this temperature because captive mackerel had spawned at this temperature during a preliminary study. The flow rates were 32 liters min for the indoor tanks and 50 liters min for the outdoor tank. Each tank also had a recirculating pump of 250 liters min capacity.

Each of the experimental groups contained 50 fish. Commencing on 17 March, the three groups of fish in the indoor tanks were maintained on photoperiods of 4L20D, 8L16D, and 16L8D, respectively. The group of fish in the outdoor tank remained under the natural photoperiod where the time between sunrise and sunset was 12 h. Biopsy samples of the gonads were taken prior to the photoperiodic change and again a month later to note the change in maturation. The biopsies were taken by inserting the tip of a glass pipette (1.2 mm in diameter) through the genital pore of a fish anesthetized in 7 ppm quinaldine and removing a small piece of gonad by mild suction. The technique, a modification of that used by Stevens (1966), did not appear to cause permanent damage to the fish. All ovarian samples were examined with a dissecting microscope and the diameter of the largest eggs measured to the nearest 0.1 mm. No effort was made to categorize the males except to note if milt was obtained. Six females were biopsied at the start of the trial and two from each treatment at the end.

An egg strainer was positioned at the outflow of each tank and inspected daily to detect spontaneous spawning. The strainer, a 1 × 1 × 0.2 m wooden frame with 202-μm mesh netting stretched across the bottom, was partially immersed in a water bath to prevent desiccation of eggs. The mackerel were fed daily with either freshly thawed frozen anchovies or ground squid. Occasionally, Oregon moist chow was mixed in with the ground squid as a supplement. The estimated daily ration was 4% of body weight.

Maturation of Mackerel Under Ambient, 15°C, and 18°C Temperatures

Mackerel judged to be in or near postspawning condition were collected between 23 August and 28 September 1973. The fish ranged from 330 to 370 mm fork length and were kept indoors at 18°C-14L10D during the period of collection. The mackerel were subsequently divided into three groups of 50 fish each and placed in two of the indoor pools and in the outdoor pool already described. Beginning on 3 October, the two groups of indoor fish were kept at 15°C and 18°C, respectively. The fish in the outdoor tank received seawater at ambient temperature (19°C at the outset) which fluctuated with ocean conditions at the intake. The intake was located at the end of the pier at the Scripps Institution of Oceanography, La Jolla. The photoperiods were 14L10D for both indoor groups and natural for the outdoor group. Six females were biopsied at the start of the trial for ova measurements. Several fish from each group were biopsied at various intervals afterwards until March 1974 to observe changes in ovarian development. I attempted to obtain eggs from at least two females per group with every round of sampling.

Test of a 16°C-14L10D Environment for Maintaining Mackerel in Spawning Condition After the Normal Spawning Season

The group of 50 fish that was held outdoors under ambient conditions began to spawn spontaneously at the end of April 1974. On 7 July, while some spawning was still in progress, 25 fish were transferred indoors to a tank with ambient temperature (19°C) seawater and photoperiod of 14L10D. On 8 July, the temperature was lowered to 16°C and the fish were kept at that temperature for 9 mo. Biopsies were taken at the time of transfer and in each succeeding month to determine if at least one female was in spawning condition. During each sampling, fish were catheterized until a female with 0.7-mm diameter eggs was found. Females with eggs of this size are functionally mature, i.e., can be spawned with hormone injections.

Testing of Hormones for Induction of Spawning

The agents tested for the induction of spawning were gonadotropin from ground chinook salmon, *Oncorhynchus tshawytscha*, pituitary (SP), human chorionic gonadotropin (HCG), and gonadotropin from pregnant mare serum (PMS). The agents were applied individually and in combination, as indicated in Table 1.

The salmon pituitaries were collected, preserved, and prepared as described by Haydock (1971). The carrier for all injections was saline and the injection volume 0.1 ml. The injections were applied intramuscularly near the base of the dorsal fin with a 24-gauge needle on a 0.5-ml syringe.

The mean weight of the fish was 0.9 kg (range 0.8 to 1.1 kg). Dosages were not adjusted for differences in fish weight, and one male and one female were injected for each treatment. The fish had become sexually mature in the laboratory and were among those used in the photoperiodic experiment. The injection trials were carried out during June through August which is also the time of spawning in nature.

Fish were biopsied beforehand and only males with generous amounts of milt and females with 0.7-mm diameter eggs were injected (preliminary testing indicated that the eggs had to be close to 0.7 mm in diameter before the hormones would stimulate a noticeable response). The injected pair was isolated in a small swimming pool (3 m in diameter, 0.5 m water depth) with water temperature at 17°C and a flow rate of 2.5 liters/min. An egg strainer was placed at the outflow to detect spawning. Biopsies and general observation were

TABLE 1.—Results of tests with gonadotropin from ground salmon pituitary (SP), human chorionic gonadotropin (HCG), and gonadotropin from pregnant mare serum (PMS) for induction of spawning in *Scomber japonicus*.

Hormones and dosages				After 24 h[2]						After 40 h						Results of stripping[4]	
First injection		Second injection[1]															
Hormone	Dosage	Hormone	Dosage	Egg diameter[3] (mm)	Not ovulated	Ovulated	Spawned	Female dead	Female alive	Egg diameter (mm)	Not ovulated	Ovulated	Spawned	Female dead	Female alive	Number eggs	Number live larvae
SP	1 mg	—	—	0.8	X				X	1.1		X			X	<500	<10
SP	5 mg	—	—	0.8	X				X	1.1		X		X		—	—
SP	10 mg	—	—	1.1		X		X						—		—	—
SP	15 mg	—	—	1.1		X			X					X		<500	<10
SP	25 mg	—	—	0.9	X				X	1.1		X		X		—	—
HCG	12.5 IU	—	—	0.8	X				X	1.1		X			X	<500	<10
HCG	25 IU	—	—	0.8	X				X	1.1		X			X	<500	<10
HCG	50 IU	—	—	0.9	X				X	1.1		X		X		—	—
HCG	125 IU	—	—	1.1		X		X						—		—	—
HCG	250 IU	—	—	1.1		X			X					X		<500	<10
HCG	500 IU	—	—	1.1		X			X					X		<500	<10
PMS	300 IU	—	—	0.8	X				X	0.8	X				X	—	—
PMS	750 IU	—	—	1.1		X			X						X	<500	<10
PMS	1,000 IU	—	—	0.8	X				X	1.1		X			X	5,000	<10
SP	1 mg	PMS	100 IU	0.9	X				X	1.1			X		X	50,000	10,000
HCG	12.5 IU	PMS	100 IU	0.8	X				X	1.1			X		X	30,000	10,000
SP + HCG	1 mg 12.5 IU	SP + HCG + PMS	1 mg 12.5 IU 200 IU	0.9	X				X	1.1			X		X	80,000	30,000

[1] Second injection given 24 h after first injection.
[2] Time measured after first injection.
[3] Egg diameter was 0.7 mm before first injection.
[4] Stripping was attempted on live fish with ovulated eggs. Stripping was attempted even if a fish spawned because the eggs were unfertilized.

taken at 24 and 40 h after injection to note the effects of the hormones. If ovulation or spawning had occurred, stripping was attempted and the eggs fertilized by the dry method (Davis 1961).

RESULTS

Maturation of Mackerel Under Four Photoperiods

The female mackerel caught before the spawning season became mature in the laboratory under the three constant photoperiods (4L20D, 8L16D, and 16L8D) and under ambient light conditions. At the start of the experiment (17 March) the diameter of the largest eggs sampled from the six females ranged from 0.4 to 0.6 mm. Thus, the females were not fully mature but two of the males sampled already had milt and may have been capable of spawning. Recently spawned eggs appeared in the egg strainer of the 16L8D tank on 17 April, 1 mo after the beginning of the experiment. Catheterization of two females from each treatment showed that all treatments contained females with 0.7-mm diameter eggs indicating sexual maturity. None of the treatments appeared to inhibit maturation. The results indicated that female mackerel in prespawning condition will become sexually mature in the laboratory under a wide range of photoperiods at 19°C.

The dates of initial spawning showed no relation to the length of day. Spawning was detected in the 4L20D tank on 25 April and in the outdoor tank on 1 May 1973. In the outdoor tank, the time between sunrise and sunset had lengthened from 12 h at the start of the trial to 13½ h on 1 May. Spawning was never detected in the 8L16D tank although it contained functionally mature males and females.

The mackerel spawned during the dark period but the exact time is not known. Watanabe (1970) stated that mackerel spawn between 2000 and 2400 h in nature. Spawning occurred three or four times a week in the outdoor pool and two or three times a week in the indoor pools from May to mid-June. The frequency of spawning then decreased and was rare by mid-July when observations ended.

Although the fish spawned spontaneously, the predictability of spawning and the viability of eggs were not satisfactory. The number of eggs collected per day was usually less than 3,000, although one collection was over 50,000. The percentage of viable eggs seldom exceeded 10% and was often zero. The spontaneously spawned eggs were translucent and of the proper size, 1.1 mm in diameter, but most were not fertilized.

Observations ended in mid-July because the fish began to feed poorly and started to die. An accompanying symptom of failing health was the malformation of jaws in about half of the fish. Afflicted fish swam with their jaws constantly agape and were unable to bite on food items. The condition may have been partly due to the high water temperature as some fish recovered when transferred to a tank with 15°C seawater. Thus, while the mackerel became fully mature at 19°C a prolonged exposure may be detrimental.

Maturation of Mackerel at Ambient, 15°C, and 18°C Temperatures

Mackerel captured near the end of the spawning season redeveloped their ovaries more rapidly at 18°C than at 15°C or ambient temperature (Figure 1). Three of the females sampled at the start of the trial, 3 October, had eggs 0.7 mm in diameter while three others had eggs 0.2 mm in diameter. This difference in egg size can be expected near the end of the spawning season as some females stop spawning and begin resorption of ovaries earlier than others. In November, one female from the 18°C treatment still had eggs 0.7 mm in diameter but four other fish from that treatment and five from each of the other two treatments could not be sexed because of immaturity of the gonads. Below a certain stage of maturity gonads are too small to remove tissue for biopsy. Biopsies were still difficult to perform in January and samples were obtained from less than half of the fish. The females that did provide samples had eggs measuring 0.3 to 0.4 mm in diameter. Biopsies were more successful in February; the females from the 15°C and ambient temperature groups still had eggs measuring 0.3 to 0.4 mm in diameter but two females from the 18°C group had eggs of 0.5 and 0.6 mm in diameter, respectively. Two of the three females sampled from the 18°C group on 20 March had eggs of 0.7 mm in diameter and one was spawned with hormone injections. The spawning date was about 5½ mo after the start of the trial. On 20 March, the females from the 15°C and ambient temperature groups did not as yet have eggs exceeding 0.5 mm in diameter. Observations ended shortly after for the 15° and 18°C

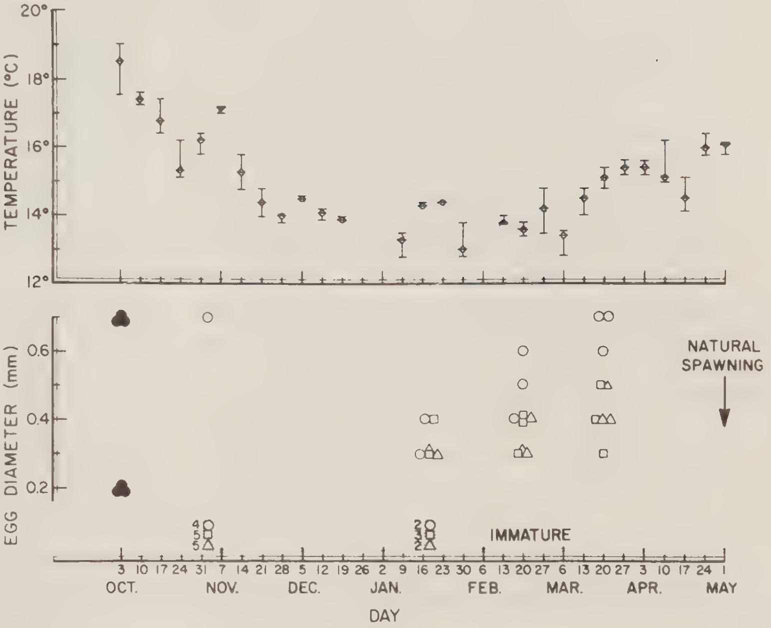

FIGURE 1.—Development of eggs in female *Scomber japonicus* under three temperature conditions. Upper panel, weekly ambient temperature ranges and medians. Lower panel, diameter of the largest eggs in individual females under 18°C, 15°C, and ambient temperatures. Shaded area, numbers of individuals which could not be sexed due to immaturity. Closed circles represent egg diameters in initial sample, open circles at 18°C, squares at 15°C, and triangles at ambient temperature. Arrow indicates when group under ambient conditions spawned naturally.

groups because of a water system failure and total loss of fish indoors.

The fish in the outdoor tank survived and began to spawn spontaneously on 30 April, nearly 6 wk after the induced spawning. The end of April is also the approximate time that the natural population begins to spawn off the southern California coast (Kramer 1960). The temperatures in the outdoor tank were very similar to the temperatures at Scripps Pier, which can be considered indicative of surface coastal conditions off southern California (Radovich 1961). Thus the mackerel in the outdoor tank should have received temperatures which were like the temperatures found in the southern California spawning grounds and the similar time of initial spawning may be expected. However, it should be pointed out that mackerel in the wild can migrate over long distances (Roedel 1952) and the average temperature cycle they undergo in nature is not precisely known.

The temperature in the outdoor pool at the time of initial spawning was 16°C which is a favorable temperature for mackerel spawning in nature. Kramer (1960), utilizing data from the California Cooperative Oceanic Fisheries Investigations surveys, found mackerel larvae occurring at temperatures (taken at 10 m) ranging from 10.3°C to 26.8°C with more than 68% of all occurrences between 14.0° and 17.9°C. Watanabe (1970), using Japanese data, found early stage mackerel eggs occurring between temperatures (taken at the surface) of 13° and 23°C with the mode of positive stations between 16° and 19°C.

Test of a 16°C-14L10D Environment for Maintaining Mackerel in Spawning Condition After the Normal Spawning Season

The group of 25 fish that was placed under a 16°C-14L10D environment contained functionally mature individuals at the start of the trial, 7 July. Monthly biopsies indicated that at least one female in the group was sexually mature from July 1974 through March 1975. The months of sampling included December, January, and February when the maturity indices of mackerel are at the lowest levels (Knaggs and Parrish 1973). No more than three females were catheterized in any month before one with 0.7-mm diameter eggs was found. The eggs in the other females ranged from 0.2 to 0.6 mm in diameter. I am not certain if the ripe females remained sexually mature continuously or if they resorbed and subsequently redeveloped their ovaries.

Effectiveness of Hormones for the Induction of Spawning

All injections of ground salmon pituitary (SP) from 1 to 25 mg stimulated hydration and ovulation but the females did not spawn spontaneously nor could they be satisfactorily stripped (Table 1). The females ovulated within 24 h in the 10- and 15-mg trials and between 24 and 40 h in the 1-, 5-, and 25-mg trials. Ovulated eggs were catheterized from live fish in the 1- and 15-mg trials and from dead fish in the 5-, 10-, and 25-mg trials. The live females in the 1- and 15-mg trials were stripped as soon as ovulation was detected but the fish released only small numbers of eggs even with heavy stripping pressure. Attempted fertilization resulted in less than 10 larvae in both trials. The stripped eggs were translucent, measured 1.1 mm in diameter, and appeared normal but nearly all were not viable.

The females that received 5, 10, 15, and 25 mg of SP died within 40 h after injection. The female that received 1 mg was intentionally killed at 72 h for dissection. All of the females including the one that received only 1 mg of SP had severely distended abdomens. Subsequent dissection revealed that the distension was due to extremely enlarged ovaries. The ovaries contained many ovulated eggs which were not extruded and the females were apparently egg bound. I did not see any plugs or clots which impeded the flow of eggs.

All injections of SP, 1 to 25 mg, to male mackerel facilitated the stripping of milt. The milt in the catheter samples before injection was thick and only small amounts could be expressed. The injections of SP brought about a thinning of the milt and made stripping easier. None of the males injected with SP died.

All injections of human chorionic gonadotropin (HCG), 12.5 to 500 IU, stimulated hydration and ovulation but the females could not be easily stripped of eggs. Ovulation occurred within 24 h in the 125-, 250-, and 500-IU trials and between 24 and 40 h in the 12.5-, 25-, and 50-IU trials. None of the females that were alive when ovulation was detected could be stripped of more than 500 eggs. The number of larvae produced was negligible in all trials. All of the females that received 50 or more IU of HCG died within 40 h after injection. The females that received 12.5 or 25 IU of HCG were purposely killed at 72 h. As with SP, all of the females had severely distended abdomens and enlarged ovaries. All dosages of HCG facilitated the stripping of milt without killing the male.

The results of trials with pregnant mare serum (PMS) were variable. In the 1,000-IU trial the eggs increased in size from 0.7 to 0.8 mm in diameter in 24 h and were ovulated by 40 h. More than 5,000 eggs were stripped at 40 h but most of the eggs were cloudy, had collapsed perivitelline membranes, and were apparently overripe. However, a few eggs were viable and a small number hatched following fertilization. In the 750-IU trial, ovulation was detected at 24 h but the eggs already had collapsed perivitelline membranes and were overripe. The eggs in the 300-IU trial grew to 0.8 mm within 24 h but did not show further improvement at 40 h. None of the females injected with PMS had severely distended abdomens and none were dead by 40 h after injection. At all levels tested, PMS made the stripping of milt easier and did not kill the injected male.

The three combinations of hormones tested were all successful in stimulating hydration, ovulation, and spontaneous release of eggs. The first injection, 1 mg SP, of the SP-PMS trial promoted egg growth from 0.7 to 0.9 mm in diameter in 24 h. The second injection of 100 IU PMS 24 h later appeared to stimulate the release of eggs as 50,000 eggs were found in the egg strainer at 40 h. The eggs were translucent, measured 1.1 mm in diameter, and appeared to be of good quality but were unfertilized. However, the female extruded another 50,000 eggs when stripped at 40 h and these were artificially fertilized with milt from the injected male. About half of the eggs showed signs of cleavage and approximately 10,000 larvae hatched. The larvae appeared normal when compared with the larval descriptions of Kramer (1960) and Watanabe (1970). Some of the larvae later developed into juveniles which grew to more than 100 mm total length.

The other two combinations (12.5 IU HCG initially and 100 IU PMS 24 h later; 1 mg SP + 12.5 IU HCG initially and 1 mg SP + 12.5 IU HCG + 200 IU PMS 24 h later) produced similar results. The initial injection produced egg growth to 0.8 or 0.9 mm and spawning occurred after the second injection but the spawned eggs were unfertilized. The fish were then stripped and the eggs artificially fertilized. Many of these hatched and produced thousands of viable larvae. All of the females became bruised from the handling during stripping, and died a few days after spawning.

RECOMMENDED PROCEDURE

A procedure for spawning mackerel has been developed from the foregoing observations and the method has been used since March 1975 to routinely produce viable eggs. The 16°C-14L10D environment is used to ripen and maintain spawnable stocks of fish in the laboratory and hormone injections are used to induce spawning. I use 1 mg SP + 12.5 IU HCG for the first injection followed by 1 mg SP + 12.5 IU HCG + 200 IU PMS 24 h later to spawn females and a 5-mg SP injection for spawning males. I inject two males to insure an adequate supply of milt. The procedure is essentially the same as described in the Methods section. The egg strainer is checked regularly beginning at 12 h after the second injection to the female and the female is examined whenever eggs are detected. The female is stripped if she releases eggs easily and the eggs are extruded into a dry finger bowl for fertilization. The male is stripped and the milt collected with a spoon held below the genital pore. The milt is washed into the finger bowl with a little seawater and the contents swirled gently for 3 min. The eggs are then placed in an incubation tank for further development and hatching. To date, induction of spawning has been successful 26 times in 36 attempts, each spawning producing 6,000 or more viable eggs, and successful spawning has been induced during every month of the year.

ACKNOWLEDGMENT

I thank John Hunter, Southwest Fisheries Center, National Marine Fisheries Service, NOAA, for his many useful suggestions in the preparation of this paper.

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(Reprinted from Nature, Vol. 269, No. 5628, pp. 501–504, October 6, 1977)

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Pacific sea-surface temperature related to rain in California

California is experiencing the worst drought in modern history, and there is much concern and speculation about future rainfall prospects. We recently succeeded in relating South Atlantic sea surface temperatures (SST) to rain in northeastern Brazil[1], and here we use similar methods to relate sea surface temperatures over the North Pacific Ocean to rainfall in California. We found December SST in the north-east Pacific off Washington to have a limited but definite predictive value, and to account for about 45% of the variation in California rainfall for the period February–April.

Namias has published several papers relating SST in the Pacific to atmospheric circulation[2]. In our approach, aimed at obtaining a useful forecasting tool, we go directly from a contributory cause (SST) to an ultimate effect (rainfall), bypassing intervening physical processes. We justify this by the belief that rainfall is an integrator of the multitude of ocean–atmospheric interactions and processes that occur simultaneously on several scales of space and time.

We divided the rainy season into two parts, early rains (November–January), and the late rains (February–April). The months May–October are usually dry in California, and when rains do occur they are influenced by factors apart from the normal November–April rains. We did not investigate the effect of SST on rains in May–October, although SST off Baja California is almost certainly related to the occurrence of September and October rains originating from decaying *chubascos,* or west coast Mexican hurricanes.

First, we established rainfall indices (RFI) for California. Rainfall is quite highly correlated among stations over most of the state. We chose three stations: Sacramento, Fresno and Los Angeles. All have long records, and are about equally spaced along the length of California. All three stations respond only to synoptic situations that are definitely wet, and receive little moisture from marginal situations. For November–April all three stations have high correlation with the November–April RFI, *r* being 0.90, 0.92 and 0.89, for Sacramento, Fresno and Los Angeles, respectively. To give each station equal weight in the index, multipliers of 0.86, 1.26 and 0.96, derived from 1930–60 mean annual rainfall values, were used for Sacramento, Fresno and Los Angeles, respectively. The RFI for a given period is the sum of weighted rainfall for that period, in millimetres.

Interestingly, for the period 1889–1972 there is no correlation between early and late rainfall indices. Kendall's parameter τ equal to -0.07 and r to -0.02, are not significant. Thus failure of early rains does not indicate that late rains will also be deficient.

Our SST values were mean temperatures developed by NMFS Pacific Environmental Group from ship observations assembled by the National Climatic Center. These values are means of all observations taken in a given 5° quadrant in a Marsden Square, during a given month and year. They have not been corrected for space or time bias, and it would be expected that correlations obtained from them would be improved if corrections could be made. We used monthly averages of available ship observations of SST in 5° quadrants, 1931–72, for the Pacific Ocean north of 15°N latitude. Ship reports for three Marsden Squares (90, 128, 130) were not conveniently available, so these areas were not considered. The area to the south-east of Hawaii and equatorwards of 15° is probably influential in California rainfall, but SST data there are too sparse for analysis. Elsewhere, data exist in most quadrants for most years, except 1941–46. In preparing our correlation maps, we used all values that were averages of four or more observations in a given month and quadrant, except a few extreme coldest and warmest values based on less than 10 observations were excluded.

In our work relating rain in Brazil to SST in the South Atlantic Ocean we found a slight warming trend of 0.0078 °C per yr for the period 1907–72, and had assumed that this warming was due to instrumental error resulting from evaporative cooling from bucket samples in early years, and heating by ships' engines in injection temperatures in later years. Removal of this trend improved correlations with rainfall. We had originally intended to adjust the North Pacific SST data for the same reason, but soon found that the trend was generally much larger and more variable in space and time than could be accounted for by instrumental factors. We therefore added an arbitrary 0.01 °C per yr before 1972, to compensate partially for the warming trend. Corelations obtained when temperatures are so adjusted are higher than when the raw data are used, which suggests that some degree of instrumental warming may be real.

We found little significant or useful correlation between Pacific SST and November–April rainfall, although there is a tendency towards negative correlation extending from the central Pacific to the region south-east of Japan. In general, the cold water there tends to make California rainy.

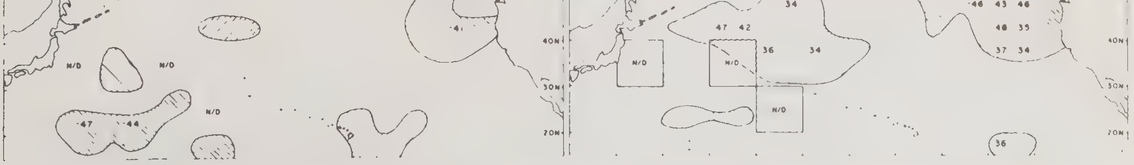

Fig. 1 Correlation between SST and November–January rainfall in California. Correlation coefficients plotted when significant above the 0.05 level.

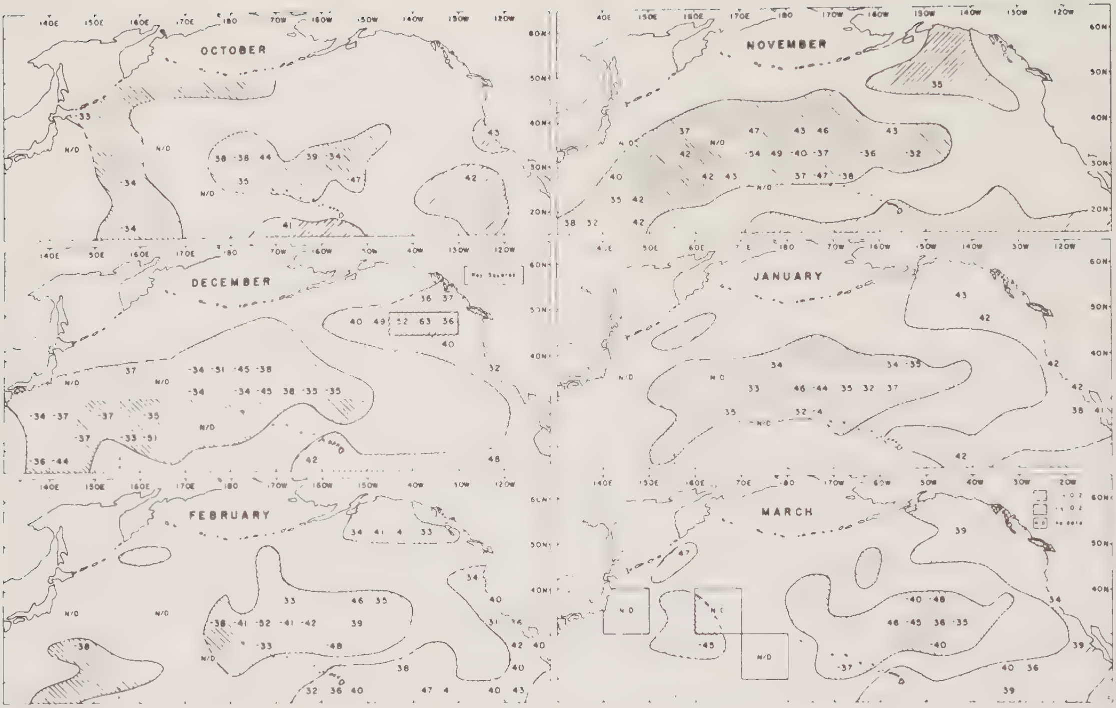

Fig. 2 Correlation between SST and February–April rainfall in California. Correlation coefficients plotted when significant above the 0.05 level.

We found no useful forecasting relation between Pacific SST and November–January rainfall, however, these rains are accompanied by negative correlation—cold water off the coast (Fig. 1). This substantiates Namias' view that warm water off the coast was involved in the 1976–77 winter drought in California[3].

A useful forecasting relation seems to exist between SST and February–April rainfall. The situation begins with negative correlation (cold water) in the western and central parts of the Pacific in October. Later in November, December and January, positive correlation (warm water) appears in the Gulf of Alaska. This progresses southwards in February and March, while cold water remains a short distance out to sea (Fig. 2). The area of positive correlation in the north-east Pacific off Washington in December seems to offer the most promise in forecasting February–April rains. In this area MS 158-4 has a correlation coefficient (r) of 0.63 between December SST and February–April rainfall, significant above the 0.001 level. It seems that processes induced by cold water in the central and western Pacific in October, November and December, when followed by warm water west of Washington in

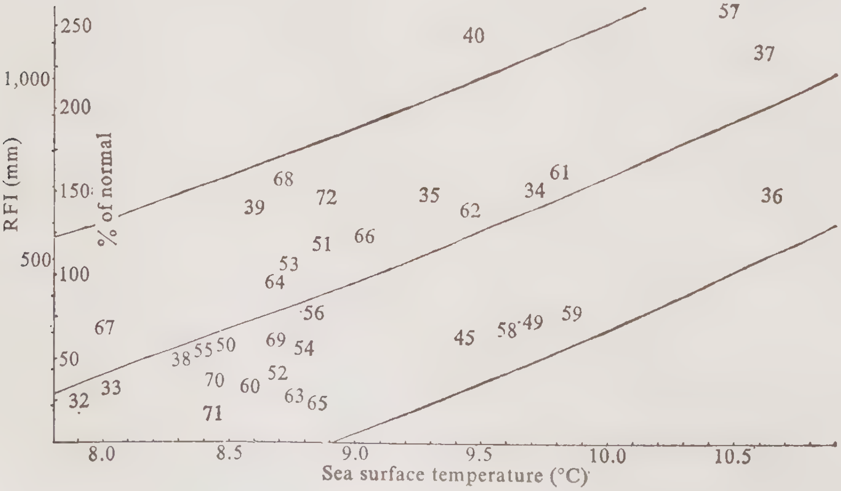

Fig. 3 February–April California rainfall indices (RFI) plotted against corrected December SST in Marsden Square 158–4. Normal SST is 9.04 °C and RFI is 459 mm. Years indicated are for SST. Second degree regression line with 95% confidence limits is shown.

December, are favourable to February–April rains in California. This implies that SST gradient between the two areas is important although we found that this gradient does not yield correlation coefficients as high as using SST at MS 158-4 directly.

Mean SST values for a given month and quadrant contain real SST variations, as well as considerable noise due to non-random distribution of observations in space and time and to various instrumental errors. This noise can be reduced by using a median anomaly from three adjacent quadrants, using those quadrants most nearly aligned with the isotherms of SST. The median is a better measure than the mean because of the effect of extreme values on the mean. The three-quadrant median deviation is taken as the corrected deviation from normal for the central quadrant. Table 1 illustrates the derivation of corrected SST values for MS 158-4.

When monthly SST values in MS 158-4 are refined as stated above, by introducing data from adjacent quadrants, $r=0.68$ and $\tau=0.50$, both with massive significance. This provides the basis for a February–April rainfall forecast using December SST (Fig. 3). Normal is defined as the mean for the 34 yr during the period 1931–72 when data exist in all three quadrants. When SST is normal, the rainfall forecast will be for 100% of normal, with 95% confidence limits between 10% and 190% of normal. If SST is 1 °C above normal, the rainfall forecast is for 160% of normal, with 95% confidence limits between 65% and 250%. If SST is 1 °C below normal the rainfall forecast is for 40% of normal, with 95% confidence limits between 0% and 135% of normal. The confidence limits are unfortunately wide, but probably reflect with reasonable accuracy the limits set by SST upon rainfall. Although imprecise, it is an improvement over a forecast based on

Table 1 Derivation of corrected SST for MS 158–4 (°C × 100)

Year	SST for MS 158–4 Raw value	SST for MS 158–4 Adjusted*	Deviation MS 159–3	Deviation MS 158–4	Deviation MS 158–3	Correction†	Corrected SST MS 158–4
1931	824	865		−48	22		
32	750	790	−126	*−123*	−7	0	790
33	736	775	−80	−138	*−110*	28	803
34	900	938	94	25	*62*	37	975
35	894	931	14	*18*	95	0	931
1936	1018	1054	158	141	*154*	13	1067
37	1029	1064	212	*151*	−42	0	1064
38	797	831	116	*−82*	−154	0	831
39	829	862	58	*−51*	−76	0	862
40	900	932	*35*	19	43	16	948
1941	—	—	—	—	—	—	—
42	—	—	—	—	—	—	—
43	—	—	—	—	150	—	—
44	—	—	—	—	190	—	—
45	916	943	116	*30*	−28	0	943
1946	—	—	165	—	—	—	—
47	—	—	—	—	—	—	—
48	—	—	−93	—	−209	—	—
49	947	970	8	*57*	94	0	970
50	897	919	*−65*	6	−91	−71	848
1951	906	927	*−24*	14	−38	−38	889
52	843	863	*−44*	−52	7	6	869
53	831	850	*−39*	−63	−27	24	874
54	877	895	−46	−18	*−32*	−14	881
55	823	840	2	*−73*	−90	0	840
1956	844	860	29	−53	*−32*	21	881
57	1034	1049	209	136	*137*	1	1050
58	953	967	−3	54	*51*	−3	964
59	1012	1025	33	112	*75*	−37	988
60	848	860	−120	*−53*	104	0	860
1961	1078	1089	12	176	*70*	−106	983
62	1079	1089	−22	176	*35*	−141	948
63	787	796	*−35*	−117	−21	82	878
64	958	966	−93	53	*−41*	−94	872
65	878	885	−44	*−28*	10	0	885
1966	901	907	8	*−6*	−11	0	907
67	798	803	−125	*−110*	−78	0	803
68	871	875	−105	*−38*	−22	0	875
69	867	870	−63	*−43*	−8	0	870
70	878	880	−70	−33	*−67*	−34	846
1971	845	846	−52	*−67*	−93	0	846
72	948	948	*−21*	35	−22	−56	892
n	35	35	36	35	38		34
Mean SST	894	913	862	913	996		904
r	0.593	0.628					0.668
t	4.23	4.63					5.07
α''	<0.001	<0.001					<0.001
φ	0.441	0.482					0.509
z	3.73	4.07					4.24
α''	<0.001	<0.001					<0.001

Median values are italicised.
*0.21 °C added for each year before 1972.
†Difference between MS 158–4 deviation from normal and three square median deviation from normal.

climatic normals, which would be for 100% of normal with 95% confidence limits between 10% and 190% of normal, regardless of SST.

The τ value of 0.50 implies that the odds are three to one that a change in rainfall will match the sign change in SST.

We believe that, early in the season, cold water in the central Pacific induces greater-than-normal troughing in the overlying atmosphere. This induces an increased frequency of south-westerly winds that push the SST isotherms northwards in the Gulf of Alaska. As winter advances the cold anomaly in the central Pacific is advected slowly eastward. Troughing in the atmosphere may likewise move eastward, and act to decrease the intensity of the surface subtropical high pressure cell off the California coast. The resultant decreased north-westerly winds along the coast allows a warm SST anomaly to form by decreased upwelling and by reduced southward flow of the California Current. The warm water moves southward, and then westward with the North Equatorial Current as the season advances, to create a positive anomaly of SST near Hawaii. Namias has shown that warm water in this area is important for California moisture[4]. Our speculation is tenuous, but we hope that other researchers will study the cause and effect relationships underlying what seems to be real correlation between SST and California rainfall.

We thank Jerome Namias for comments, Jim Canfield for cartography and Martha Raught for typing.

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Received 20 June; accepted 31 August 1977.

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Printed in Great Britain by Henry Ling Ltd., at the Dorset Press, Dorchester, Dorset

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(Reprinted from Nature, Vol. 265, No. 5592, pp. 320–323, January 27, 1977)

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Sea surface temperature related to rain in Ceará, north-eastern Brazil

Rainfall in Ceará is correlated with sea surface temperature in the south Atlantic Ocean. Knowledge of sea surface temperature makes possible a useful rainfall forecast before the rainy season begins. The mechanism may be that sea temperature affects the height of the trade wind inversion, and thus the height of the moist layer. The data also suggest in association between below normal sea temperatures in the south Atlantic and the El Niño in the Pacific.

Ceará is the node of Brazil's drought-prone north-east. Here severe drought, and its antithesis, flooding, both occur about once per decade, arriving without warning. The human misery that follows in their wake might be reduced if they could be forecast. We found that sea surface temperature (SST) in the south Atlantic Ocean and rainfall in Ceará are correlated in time, and if SST is known, a useful preliminary rainfall forecast can be made.

Brazilian climatologists have long believed rain in the north-east to be related to fluctuations in SST, but have been unable to show such a relationship owing to lack of sufficient SST reports. We investigated this relation by using a data file containing all available surface marine weather reports from ships of many nations. This file, Tape Data Family -11, was assembled by NOAA's National Climatic Center. Working in conjunction with the Fleet Numerical Weather Central and the North Pacific Experiment (NORPAX) the National Marine Fisheries Service has used the tape data file to compute mean sea surface temperatures by 5° latitude-longitude quadrants for each month in the period October 1947 to December 1967. We used these computations to map the correlation coefficient between SST and a rainfall index in Ceará. Later, after we had identified a key 5° quadrant where correlation was particularly high, monthly SSTs were recomputed for the period 1907–72, and used in a regression analysis to develop a forecasting equation. Our results may be somewhat biased by the selection of this particular quadrant, and further research may show that improved forecasts can be made using data from other areas.

The density of SST observations is far from uniform over the South Atlantic. Reports are most abundant along shipping lanes between the Cape of Good Hope and Cape

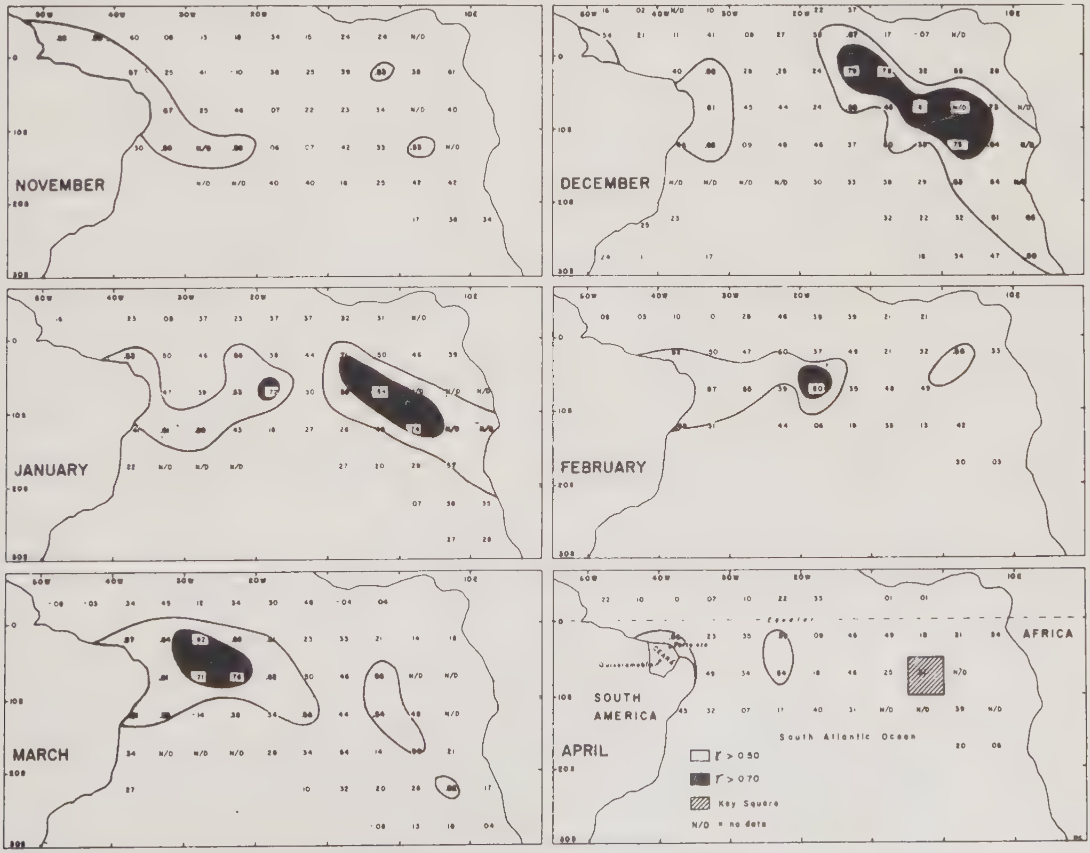

Fig. 1 Correlation between SST and January-February-March rainfall indices in Ceará. An area of high coefficient of correlation appears off the African coast in November, becomes strong in December, moves westward with the South Equatorial Current during January, February and March, and disappears in April.

Verde, and along the South American coast. Data are extremely sparse over the central South Atlantic, and are not sufficient to map correlation coefficients over the entire area. Data are not available in all quadrants in all years, and different years are missing from different quadrants. Nevertheless, when considered as a whole, the data form a picture that is coherent and of predictive value.

The rains in Ceará are highly seasonal, about 40% coming in January-February-March, and about half in April-May-June. Almost no rainfall occurs in the months August to November. Fortaleza and Quixeramobím are two weather stations in Ceará about 120 km apart that have long series of rainfall observations extending back to 1849 and 1896, respectively. We correlated monthly mean SST data with rainfall at both stations, but found that a combined index of simultaneous data from both stations gave higher correlation coefficients. The combined index smooths local variations of rainfall to emphasise large scale influences affecting both stations. Since the mean annual rainfall at Fortaleza, on the coast, is about twice that of Quixeramobím, in the interior, we gave each station equal weight in the index by using twice Quixeramobím's rainfall plus Fortaleza's.

We computed correlation coefficients (*r*) for each of the 5° quadrants in the South Atlantic for which data are available, between the monthly values of SST and the rainfall index for the combined months of January-February-March, as well as for the annual rainfall indices. SSTs for November and December were correlated with rainfall indices for the coming year, while SSTs for January through April were correlated with the current year.

Maps of correlation coefficients (Fig. 1) show an apparent westward movement of high correlation during November to April. This may be related to the westward drift of water in the South Equatorial Current. In December the quadrant where correlation is highest is centred at 7°30′S, 2°30′W (Marsden Square 300, Quadrant 3). For this area *r* was 0.81 for January-February-March rainfall, and 0.73 for annual rainfall. Ceará tends to be dry when water here is cold, and wet when it is warm. Moreover, since December precedes the rainy season in Ceará, December SST can be used to forecast rainfall with useful lead time. Thus we selected Quadrant 300-3 as the key area for regression analysis with Ceará's rainfall.

The 1947-67 data used for our correlation maps are means of all reports within a given 5° quadrant and thus might be biased by clustered reports. This possible bias can be reduced by making individual means for each 1° area, then averaging the 1° means to obtain a 5° mean. This latter procedure was used to obtain data points for our long term regression analysis (Fig. 2).

We noticed a long term warming trend of 0.51 °C between the years of 1907 and 1972, in our SST means at Quadrant 300-3. The trend could be caused by real warming, or by differences in measurement techniques that have occurred over the period. If it is assumed that the latter is true, and if the effects of the trend are removed from the regression, *r* for the period increases from 0.61 to 0.66. Kendall's rank-order coefficient, τ increases from 0.20 to 0.41. This increase in order through detrending suggests that the apparent trend is instrumental and not a real warming.

Depending on the sets of data, *r* values range from 0.61 in the 1907–72 data uncorrected for trend, to 0.81 in the 1947–67 data used in making the correlation maps. Values of τ range from 0.21 to 0.50. All are for correlation

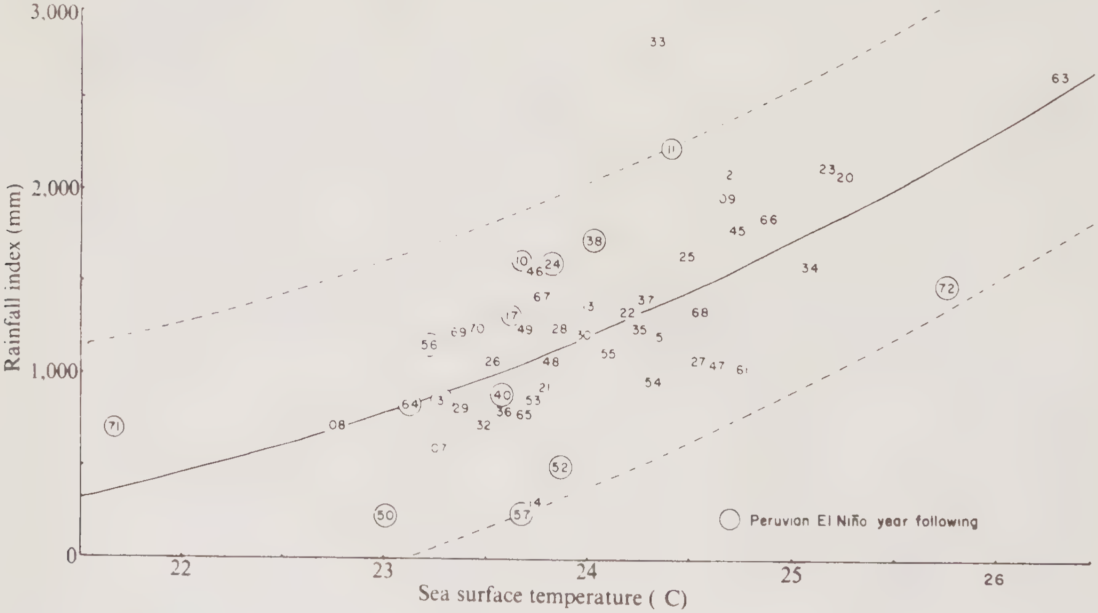

Fig. 2 January-February-March rainfall indices in Ceará plotted against December SST in Marsden Square 300, Quadrant 3. Years indicated are for December SST values. Data has been detrended by adding 0.0078 °C times the number of years before 1972. Second degree regression lines and 95% confidence limits are shown. El Niño years (taken from Caviedes (1973) and Quinn[6]) are circled.

	1907–72 Detrended	1907–72 Not detrended	1947–67 From Fig. 1
n	53	53	16
r	0.66	0.61	0.81
α	0.001	0.001	0.001
τ	0.41	0.20	0.50
α	0.001	0.04	0.007

between December SST and the Ceará rainfall index for the following January-February-March period. If we assume r to be 0.71, then r^2, the coefficient of determination, is 0.50, indicating that half of Ceará's January-February-March rainfall can be predicted by mean SST in Quadrant 300-3 in December. If we assume $\tau = 0.40$, we can say that the odds are 70/30 that a change in SST will be followed by a change in rainfall index of the same sign. Our rainfall forecast ranges from 500 mm with an SST of 22 °C to 2300 mm with an SST of 26 °C; a considerable improvement over the climatic normal value of 1267 mm. If we define drought as the lack of rainfall and flooding as an excess of it, from Fig. 2 we can state that drought is unlikely when SSTs at Quadrant 300-3 are warmer than 24.5 °C, and that flooding is unlikely when SSTs are colder than 23.5 °C. If we are given some particular SST value, say 24.0 °C, our best estimate for the rainfall index is 1200 mm, and we can say with 95% confidence that it will fall between 350 and 2050 mm. These are much wider limits than we should like but suggest that eastern Atlantic SST in December, albeit important, is only one of a number of factors influencing Ceará's rainfall.

A suggested mechanism for the correlation is as follows: cold water stabilises the overlying air and decreases wind flow and convection over the Atlantic. The trade wind inversion represents the boundary between subsiding air from aloft and convective air from below. When convection is weak and winds are light, the trade wind inversion is lowered, and the thickness of the layer carrying moisture into north-eastern Brazil is reduced. Similarly, warm seas strengthen wind flow, and mixing and increased convection raise the trade inversion to deepen the moist layer. Further, the Intertropical Convergence Zone (ITC) and its attendant raininess would tend to lie in the region of warmest water, and would retreat from the hemisphere with cold water.

Namias[1] found intense cyclonic activity near Newfoundland to be highly correlated with rain at Quixeramobím. He hypothesises the following chain of events. The North Atlantic Subtropical High is strengthened when the trough in the Newfoundland land area deepens. The trough is held in place by blocking toward the east. The strengthened subtropical High increases the north-east trade winds which in turn require the south-east trades to respond by strengthening, thus increasing the flow of moisture into Ceará. An alternative explanation for Namias' correlation is its reverse. Warm South Atlantic sea temperatures produce heavy equatorial rains. These release large quantities of latent heat, strengthening the Hadley circulation in both hemispheres, and inducing a blocking High in the North Atlantic. The increased flow from the Equator, accompanied by the blocking, results in increased cyclonic activity in the Newfoundland area, with a concurrent deepening of the trough. To support this latter explanation, Markham[2] found that a strong South Atlantic High and strong south-east trades seem to decrease, rather than increase, rain in Ceará. The rainiest periods do not occur when the south-east trades are strong, but when the High is weak or has retreated toward the south, allowing flow with a northerly component to penetrate Ceará. There is little doubt that the Newfoundland trough and rain in Ceará related, but which is the cause and which the effect is unclear. In any event, precipitation over northeastern Brazil is important to the general circulation because it represents a significant energy input to the atmosphere, and with large variations from year to year. The magnitude of this variation is shown by the annual rainfall index which varied from a low of 884 mm in 1915 to a high of 5505 mm in 1964.

From the work of Namias[3] and Bjerknes[4], a body of literature on large scale ocean–atmospheric interactions is growing. Recently Caviedes[5] has related drought in northeastern Brazil with the El Niño—the appearance of anomalously warm water off the Peruvian coast. Temperatures in Quadrant 300-3 also seem to be related to El Niño. The years preceding El Niño are circled in Fig. 2. The hypothesis that cold December SSTs precede El Niño has a one-tailed significance level of about 0.0125 when the non-parametric Wilcoxson two-sample test is applied[7]. The coldest December temperature in Quadrant 300-3, 21.67 °C in 1971, was followed by an El Niño of exceptional severity in 1972. The El Niño of 1972 may have persisted into 1973 and thus may account for the anomalous point for 1972 circled in Fig. 2. If this did occur, the correlation is greatly improved. Quinn[6] has related El Niño to the difference in surface pressures between Easter Island and Darwin, Australia. This difference is an index of the Southern Oscillation and suggests that the occurrence of warm water off Peru simultaneously with cold water off Africa is related to the Southern Oscillation. The mechanisms for this phenomenon are poorly understood.

We acknowledge the contribution of Mr B. K. Wesley Copeland, Professional Associate, Board on Science and Technology for International Development, National Academy of Sciences, whose intermediation brought us into contact.

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Received August 17; accepted December 14, 1976.

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Guide to the Identification of Scorpionfish Larvae (Family Scorpaenidae) in the Eastern Pacific With Comparative Notes on Species of *Sebastes* and *Helicolenus* From Other Oceans

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ABSTRACT

Developmental stages of 51 species or forms of scorpionfishes are described and illustrated in this identification guide. Thirty-eight are from the eastern Pacific and represent six of the eight scorpaenid genera known from that region—*Sebastes, Sebastolobus, Scorpaenodes, Scorpaena, Pontinus,* and *Ectreposebastes*. *Sebastes* is the most thoroughly treated; developmental series of six species from the eastern Pacific are described and illustrated; pigment patterns of early larvae of 33 species are given and 23 of these are illustrated. Larval series of three North Atlantic species of *Sebastes* are described and illustrated as is a series of *Sebastes* from off Chile; in addition, the published information on eight northwestern Pacific species is summarized and discussed in relation to the eastern Pacific and Atlantic species. The other genera are represented by one or two species. Since larvae of the eastern Pacific species of *Helicolenus* were not available, a larval series of *H. dactylopterus* from the Atlantic are described for comparative purposes. Larvae of the eighth eastern Pacific scorpaenid genus, *Trachyscorpia*, are unknown.

Two dichotomous keys to the eastern Pacific genera are included, one for the early larval stages up to the initiation of notochord flexion and one for postflexion larvae. In the text, a summary of the literature and definitive characters is followed by the descriptive accounts of the species. Each species account contains a literature summary, description, set of illustrations, and information on distribution and abundance.

INTRODUCTION

The scorpionfishes are among the most important groups of shore fishes in the eastern Pacific. The approximately 100 species of eastern Pacific scorpionfishes are distributed among eight genera—*Sebastes, Helicolenus, Sebastolobus, Scorpaenodes, Scorpaena, Pontinus, Ectreposebastes,* and *Trachyscorpia*. About two-thirds of the species belong to the single genus, *Sebastes*, which has undergone an extensive radiation in the northeast Pacific. These rockfishes or rockcods provide important commercial and recreational fisheries; one species alone, *Sebastes alutus*, yielded 283,000 metric tons to trawlers in a single year (Gulland 1970) and, in California, rockfishes comprise one-half of the total number of sport fish taken annually by recreational anglers (Young 1969).

The abundance of *Sebastes* is reflected in their prominence in the plankton collections of the California Cooperative Oceanic Fisheries Investigations (CalCOFI). They are live-bearers and, at birth, the 4- to 5-mm larvae rise to the surface waters where they may be sampled by plankton nets (Moser 1967a, b). As a group, they usually rank third or fourth in total abundance among all larvae collected annually by the CalCOFI plankton survey (Ahlstrom 1961). The task of identifying *Sebastes* larvae to species is a difficult one because of the large species complement of the genus; however, complete larval series of some important commercial species have been described (Moser 1967a, 1972, and in this guide). The most productive technique has been to remove late-stage embryos or prenatal larvae from identified pregnant females and to raise these in the laboratory to a point where they develop their specific pattern of melanophores. These larvae can then be used to identify developmental series of larvae from plankton collections.

During the investigation of *Sebastes* larvae, considerable knowledge of the larvae of other eastern Pacific scorpaenid genera has accumulated. One of these, *Sebastolobus*, inhabits northern waters and its larvae are found commonly in CalCOFI plankton samples from the California Current. The larvae and highly distinctive juvenile stages of *S. altivelis* and *S. alascanus* have recently been described (Moser 1974). The other eastern Pacific genera are primarily tropical-subtropical in distribution, with the exception of *Helicolenus* which occurs off southern Chile. The larvae of these warm water genera (*Pontinus, Scorpaena,* and *Scorpaenodes*) are encountered in the CalCOFI collections off southern Baja California and in the Gulf of California as well as in plankton collections from expeditions such as EASTROPAC, and each has a character or group of characters which distinguishes it from all other eastern Pacific genera. The genus *Ectreposebastes* is primarily equatorial in distribution and the larvae of *E. imus* were taken on a few EASTROPAC stations.

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It is the purpose of this paper to present information and illustrations (including keys) for the identification of the larvae of eastern Pacific scorpaenids to genus and, for each genus, to describe and illustrate the larval stages of the species for which larvae are known.

Sebastes is the most extensively treated. In addition to summaries of the earlier descriptions of *S. paucispinis* and *S. macdonaldi*, we include new descriptions of larvae of *S. jordani, S. levis, S. cortezi*, and *S.* sp. (Gulf of California Type A). Also, we describe larval series of three North Atlantic species—*S. marinus, S. viviparus*, and *S. fasciatus*. Our purpose in doing this is to supplement the already substantial literature on larvae of these species with heretofore unreported characters and to provide a basis for comparison of larvae of Atlantic and Pacific *Sebastes*. Larval series of a *Sebastes* from off Chile and eight species from Japan are described and illustrated to allow comparison of northeastern Pacific larvae with those from the Southern Hemisphere and western Pacific. Essentially we are treating *Sebastes* on a worldwide basis.

Since larvae of the eastern Pacific representative of *Helicolenus, H. lengerichi*, were not available, we include a description of the Atlantic species, *H. dactylopterus*, so that larvae of *Helicolenus* may be compared with those of other eastern Pacific genera. Many of the characters presented in this description have not been previously reported.

Larvae and juveniles of *Sebastolobus* have been thoroughly described (Moser 1974) and are briefly summarized here. The larvae of *Trachyscorpia* are unknown but if their relationships are with *Sebastolobus* as Eschmeyer (1969) suggests, then they probably will resemble the larvae of *Sebastolobus* but with lower counts of most meristics.

Life history stages of *Scorpaenodes* have not been described and we give a detailed account of larvae and early juveniles of the single eastern Pacific species, *S. xyris*. The literature contains life history accounts of three Mediterranean and North Atlantic species of *Scorpaena* and descriptions of the eggs and newly hatched larvae of a single eastern Pacific species, *S. guttata* (see literature review for the genus). We include descriptions of a complete larval series of *S. guttata* and of another *Scorpaena* not identifiable to species. Larvae of *Pontinus* have not been previously described and we describe larvae of two forms of this genus. Two larval specimens of *Ectreposebastes imus* have been briefly described (Eschmeyer and Collette 1966) and we describe a complete developmental series of this species for the first time.

Seven of the eight genera of scorpaenids that occur in the eastern Pacific also occur in the Atlantic. According to Eschmeyer (1969, 1971) who reviewed the scorpionfishes of the Atlantic Ocean, 55 of the 60 species (i.e., 92%) of Atlantic scorpaenid fishes belong to these seven genera. Since there is a strong similarity between the scorpaenid fauna of the two oceans at the generic level, the guide provides a starting point for identification of scorpaenid larvae in the tropical and subtropical Atlantic.

In addition to the genera treated in this guide, the literature contains relatively few other life history descriptions of scorpaenid fishes. We are aware of publications on only three other genera: *Pterois* (*P. lunulata*, Mito and Uchida 1958; Mito 1963), *Inimicus* (*I. japonicus*, Fujita and Nakahara 1955), and *Sebastiscus* (*S. marmoratus*, Tsukahara 1962). We are hopeful that our guide will stimulate further investigations on the developmental stages of this large and diverse family.

Relationships among the eastern Pacific genera can be shown by their groupings into subfamilies. We are following the classification presented by Matsubara (1943) and amended for the subfamily Setarchinae by Eschmeyer and Collette (1966) and Sebastolobinae by Eschmeyer (1969). The eight genera of eastern Pacific scorpaenids belong to four subfamilies, as follows:

- Subfamily Sebastinae
  - *Sebastes* Cuvier
  - *Helicolenus* Goode and Bean
- Subfamily Sebastolobinae
  - *Sebastolobus* Gill
  - *Trachyscorpia* Ginsburg
- Subfamily Scorpaeninae
  - *Scorpaenodes* Bleeker
  - *Scorpaena* Linnaeus
  - *Pontinus* Poey
- Subfamily Setarchinae
  - *Ectreposebastes* Garman

Among the primary characters for separation of adult scorpaenid fishes into subfamilies are the shape of the 2nd suborbital (3rd infraorbital) bone, whether this bone is fastened to the preopercle or remains free, and the presence or absence of 3rd and 4th suborbital bones. The suborbital sensory canal, which runs backward from the preorbital to the 2nd suborbital in all scorpaenids has a branch extending through the 3rd and 4th suborbital bones to the 5th suborbital bone in some scorpaenids. The latter branch is developed in eastern Pacific scorpaenids that retain the 3rd and 4th suborbital bones. Characters associated with the suborbital bones are summarized for the eastern Pacific genera and subfamilies in Table 1 together with meristic characters, type of reproduction, and presence or absence of a gas bladder in juveniles and adults.

MATERIALS AND METHODS

Specimens used in this study were obtained from a variety of sources. The CalCOFI plankton collections from the California Current region provided most of the larval specimens of *Sebastes* and *Sebastolobus*. CalCOFI collections from the southern end of the station pattern off Baja California and from the Gulf of California provided larvae of *Sebastes, Scorpaena, Pontinus*, and *Scorpaenodes*. Larvae of the latter three genera were also

Table 1. Characters of the four subfamilies of scorpaenid fishes in the Eastern Pacific. Counts listed are typical ones and occasionally encountered atypical counts are given in parentheses.

Subfamily	Genera	Suborbital bones			Suborbital sensory canal	Gas bladder	Type of reproduction	Vertebrae	Dorsal spines	Dorsal rays*	Anal rays*	Caudal principal rays	Caudal branched rays
		2nd	3rd	4th									
Sebastinae	Sebastes	Tapering to a point, not attached to preopercle	Present	Present	Has extension from 2nd suborbital to 5th suborbital	Present	Ovoviviparous, internal fertilization, larvae spawned	26-28 (E.Pac.) 29-32 (N.Atl.)	XIII-XIV (E.Pac.) XIV-XVI (N.Atl.)	11-17	III 5-11	8+7	6+6
	Helicolenus	Narrowed posteriorly, firmly attached preopercle	Present	Present	Same as above	Absent	Probably ovoviviparous but eggs in gelatinous mass	25	XII (XI-XIII)	11-13	III,5	8+7	6+5
Sebastolobinae	Sebastolobus	Rounded posteriorly, firmly attached to preopercle	Present	Present	Same as above	Absent	Oviparous eggs in gelatinous masses	28-31	XV-XVII	8-10	III (4)5	8+7	6+5
	Trachyscorpia	Not known	Present	Present	Same as above	Absent	Same as above	25-26	XII	8-9	III,5	8+7	6+6
Scorpaeninae	Scorpaena	Uniformly broad, or becoming wider posteriorly, firmly attached to preopercle	Absent	Present	Lacks extension to 5th suborbital	Absent	Oviparous eggs in gelatinous masses (Scorpaena)	24	XII	8-10	III 5(6)	8+7	6+5
	Pontinus		Absent	Present		Absent		24	XII	8-9	III 5(6)	8+7	6+5
	Scorpaenodes		Absent	Absent		Present		24-(25)	XIII	9-11	III 5(6)	8+7	6+5
Setarchinae	Ectreposebastes	Same as above	Absent	Absent	Same as above	Absent or rudimentary	Oviparous	24	XII	9-10	III 5(6)7	8+7	6+6

*Last soft ray of doral and anal fins is a double ray and is counted as a single ray.

found in plankton collections of the wide-ranging EASTROPAC expeditions (Ahlstrom 1971, 1972) and in collections from cruises of the Scripps Tuna Oceanography Research (STOR) group (Blackburn et al. 1962). Pelagic and benthic juveniles were obtained largely from ichthyological collections of the Scripps Institution of Oceanography (SIO) and the Los Angeles County Museum (LACM). Larvae and juveniles of *Sebastes marinus, S. viviparus,* and *Helicolenus dactylopterus* were obtained from the collections of the *Dana* Expeditions at the University Zoological Museum, Copenhagen. A series of *Sebastes fasciatus* larvae from the American coast between lat. 38°52′N and lat. 44°22′N were supplied by the National Marine Fisheries Service (NMFS) Laboratory at Narragansett, R.I., and a collection of intraovarian larvae from this species was obtained from the NMFS Laboratory, Woods Hole, Mass.

Methods of analyzing meristic and morphometric development follow Moser (1967a, 1972, 1974), however some of the terms used in this study require further explanation. The larval stage of teleosts can be divided naturally into three substages based on the state of development of the caudal fin. The substage beginning with the termination of the yolk-sac stage and ending with the initiation of notochord flexion we call preflexion. The substage from the initiation of notochord flexion to its completion, when the posterior edge of the hypural plate arrives at a vertical position, we term flexion. From this substage to the initiation of transformation is termed postflexion. These substages provide a practical means of comparing larval development in different taxa.

The change from larva to juvenile is termed transformation or transition. The juvenile stage may also be subdivided. Many scorpaenid species have a pelagic juvenile substage that is marked by a distinctive pigment pattern of bands and/or saddles and often by structural features such as enlarged pectoral fins. When pelagic juveniles become benthic juveniles there is usually an abrupt change in pigment pattern and morphometry (e.g., *Sebastolobus altivelis*). In species which remain pelagic for much of their juvenile stage (e.g., *Sebastes jordani*) there is no abrupt change in pigment or morphometry.

In discussing distribution and abundance we use the term standardized number of larvae. This means the absolute number of specimens per tow adjusted to the number under 10 m² of sea surface (Kramer et al 1972).

SUMMARY OF LARVAL CHARACTERS OF SCORPAENIDAE WITH EMPHASIS ON THOSE IMPORTANT IN IDENTIFYING GENERA

The most salient characteristic of scorpionfish larvae is their elaborate head spination. In addition to marked development of spines on the preopercle, a feature shared with many families, the larvae develop a pair of crestlike parietal ridges that terminate in a single or double spine. This parietal spination differentiates scorpaenid larvae from those of most other teleost families. Larvae of the Triglidae, a related family, also have parietal crests, but these have scalloped margins and are supported by rodlike structures. The parietal crests in scorpaenids typically have a serrate margin and have a single strengthening rod at the posterior terminus.

In *Sebastes* the paired parietal spines on top of the head develop in larvae 6.0 to 7.0 mm in length, and by the midlarval period each projects backward from a serrated parietal ridge. Later in the larval period, a smaller nuchal spine usually develops adjacent and posterior to each parietal spine. In *Sebastolobus* and *Scorpaenodes*, the nuchal spines form soon after the parietals and rapidly become larger and more prominent than the parietals. This difference in size of the nuchals relative to the parietals is especially useful in separating larvae of *Sebastes* from those of *Sebastolobus*.

Spines also form on a number of head bones in addition to the parietals, e.g., the pterotics, frontals, nasals, and circumorbitals (Moser 1972). Head spination is best developed on postflexion larvae and is a primary character in the key to postflexion larvae. Although they begin to form on late preflexion larvae, head spines are seldom differentiated enough to be used for identifying larvae to genus before flexion is completed.

As in other families, meristic characters are essential in identifying larvae of scorpionfish to genus and species. The most fundamental meristic character is the number of myomeres, since it is the earliest to appear and is equivalent to the number of vertebrae that will develop. The temperate or boreal genera (*Sebastes, Sebastolobus, Helicolenus*) have higher counts than the tropical-subtropical genera (*Scorpaena, Scorpaenodes, Pontinus, Trachyscorpia, Ectreposebastes*) as summarized in Table 2.

Characters of the fins, including numbers of spines and rays, relative size, shape, and pigmentation are indispensable in identifying scorpaenid larvae. The pectorals are the first to appear and are usually the first in which ossified rays are formed, followed by ossification of principal caudal rays, rays and spines in the pelvics, dorsal and anal fins, and finally procurrent caudal rays. Ossified rays begin to form in the pectoral fins prior to notochord flexion; they form sequentially from the dorsal to the ventral margin. The 15 principal caudal rays and pelvic rays (I, 5) form during flexion, whereas the dorsal, anal, and procurrent caudal rays begin to ossify during late flexion and early postflexion stages. The complete complement of pectoral rays forms within a 3-mm size range whereas the pelvic, dorsal, and anal fins form within a 2-mm size range; only the formation of procurrent caudal rays is extended over a greater range of length.

The number of pectoral rays is not particularly useful in distinguishing among most genera of scorpaenids. Most genera dealt with in this report have 16 to 20 rays. The only striking exceptions are one species of *Sebastolobus* with 21 to 24 rays and *Trachyscorpia* with about 22 to 23 rays.

The size, shape, and pigment pattern of the pectoral fins are useful in distinguishing among genera and species of scorpaenids (see key to genera for postflexion larvae). Especially useful is the depth of the fin base, which is narrowest in *Sebastes*, widest in *Ectreposebastes*, and of intermediate depths in the other five genera. Values for this previously unutilized character are summarized by species and stage of development in Table 3.

There is a marked range in the proportional size of the pectoral fin among the genera included in this study. Larvae of *Ectreposebastes* have huge fan-shaped pectorals which extend posteriad to the base of the caudal fin; they increase in relative length during development to a maximum of one-half the body length (Table 3). The fan-shaped pectorals in *Scorpaenodes* are only slightly smaller than in *Ectreposebastes*, attaining a maximum of 45% of the body length. The pectorals in *Sebastolobus* and *Pontinus* are moderately large but differ strikingly in shape, being fan-shaped in the former and aliform in the latter. In *Scorpaena* they are fan-shaped and moderate in

Table 2. Meristics for scorpaenids included in this guide.

						Caudal Rays			
								Procurrent	
	Vertebrae	Dorsal Spinous Rays	Dorsal Soft Rays	Anal Soft Rays	Pectoral Rays	Principal	Branched	Sup.	Inf.
Sebastes jordani	27	XIII	13-16	8-11	19-22	8+7	6+6	13-14	13-14
" levis	26	XIII	12-13	6-7	17-18	8+7	6+6	11	11
" macdonaldi	26	XIII	13-14	7-8	18-20	8+7	6+6	13-14	13-14
" paucispinis	26	XIII	13-15	8-10	15-16	8+7	6+6	12-13	12-14
Sebastes cortezi	26	XIII	11-12	5-6	17-19	8+7	6+5	10-11	11-12
" capensis	26	XIII	12-14	5-6	18-20	8+7	6+6	?	?
Sebastes marinus	30-32	XIV-XVI	12-15	7-9	18-20	8+7	6+6	11-12	11-12
" viviparus	29-31	XIV-XVI	13-14	6-8	17-19	9+7	6+6	?	?
" fasciatus	30-31	XIV-XVI	12-15	6-8	17-20	8+7	6+6	?	?
Helicolenus dactylopterus	25	XII	11-13	5	17-20	8+7	6+5	11	10-12
Sebastolobus alascanus	30-31	XV-XVII	9-10	(4)5	21-22	8+7	6+5	8-10	8-9
" altivelis	28-29	XV-XVI	8-10	5	22-24	8+7	6+5	6-8	7-8
Trachyscorpia sp.	25	XII	9	5	22-23	8+7	6+6	5	6
Pontinus Type A	24	XII	8-9	5(6)	18-19	8+7	6+5	6	6-7
" Type B	24	XII	9	5	17-19	8+7	6+5	5-7	5-7
Scorpaena guttata	24	XII	8-10	5-6	17-19	8+7	6+5	6-8	7-9
" Type A	24	XII	8	5	19-20	8+7	6+5	5	5
Scorpaenodes xyris	24-25	XIII	9-11	5-6	16-19	8+7	6+5	4-5	4-5
Ectreposebastes imus	24	XII	9-10	5-7	18-20	8+7	6+6	6-7	6-7

Table 3. Depth of pectoral fin base and length of pectoral fin relative to body length for larvae of seven scorpaenid genera, expressed as mean percentage and range for three larval stages.

Species	Number specimens	Depth of pectoral fin base						Length of pectoral fin					
		Preflexion		Flexion		Postflexion		Preflexion		Flexion		Postflexion	
		x̄	range	x̄	range	x̄	range	x̄	range	x̄	range	x̄	range
Sebastes paucispinis	21	9.0	8-10	9.0	8-10	7.2	5- 8	16.4	11-21	27.2	25-31	35.5	34-37
macdonaldi	26	-	-	-	-	-	-	8.4	6-10	13.0	12-15	19.3	15-26
jordani	23	6.7	6- 7	7.8	7- 8	7.8	7- 9	6.6	6- 7	8.4	7-10	14.7	11-20
levis	12	8.0	-	12.8	12-14	11.7	11-12	9.0	-	34.9	24-46	43.3	41-45
cortezi	17	9.0	7-10	11.8	11-12	10.8	10-12	8.2	7- 9	10.6	9-12	17.5	11-21
Gulf Type A	13	7.8	5- 9	12.3	11-13	12.8	11-14	8.7	6-10	13.3	11-16	16.8	14-20
capensis	8	14.7	8-13	14.0	12-16	12.7	10-17	10.0	9-11	15.5	12-19	23.7	18-27
marinus	22	6.7	4- 8	8.2	8- 9	8.3	7- 9	6.0	3- 7	9.9	8-13	16.8	14-19
viviparus	14	7.5	6- 9	9.6	8-11	-	-	7.3	6- 9	9.9	8-12	-	-
fasciatus	14	6.8	6- 9	8.7	8- 9	8.7	8- 9	6.2	6- 7	8.0	6-10	15.3	13-18
Sebastolobus alascanus	40	11.0	6-15	15.8	13-19	14.4	13-16	12.7	7-17	22.2	19-25	29.0	26-31
altivelis	48	11.0	6-15	15.8	13-19	18.3	15-20	12.7	7-17	22.2	19-25	35.0	28-39
Helicolenus dactylopterus	16	11.0	9-12	12.5	12-13	12.4	10-14	11.4	11-12	14.8	13-16	18.0	16-20
Scorpaenodes xyris	36	15.0	8-18	18.7	17-20	18.0	16-21	22.2	10-28	34.2	29-41	39.0	36-45
Scorpaena guttata	16	13.8	8-16	16.0	15-17	15.9	14-17	15.4	7-22	20.8	19-22	21.7	18-23
Type A	18	13.8	12-15	14.6	13-16	17.3	16-18	12.2	10-15	16.2	15-18	20.7	19-23
Pontinus Type A	22	15.3	15-16	15.5	15-16	14.3	12-16	20.4	18-19	26.5	26-27	30.7	27-36
Type B	4	-	-	17.5	17-18	16.0	14-18	-	-	33.5	33-34	27.0	24-30
Ectreposebastes imus	12	20.4	19-22	22.0	-	21.0	19-22	32.6	24-38	38.0	-	44.4	37-49

relative length and in *Helicolenus* they are small and rounded. In *Sebastes* there is a great variety in relative size and shape among the numerous species. Also, different species attain maximum relative pectoral length at different developmental stages (Table 3).

Patterns of melanistic pigmentation on the pectorals are useful in identifying larvae to genus and species as demonstrated in the key to preflexion larvae. The patterns are too diverse to be summarized here and are best treated in the succeeding sections.

Anal fin ray counts are not of particular value in distinguishing among most genera of scorpaenids. The usual anal fin count is III, 5 (occasionally III, 4 or III, 6) in *Sebastolobus*, *Trachyscorpia*, *Helicolenus*, *Scorpaenodes*, *Scorpaena*, and *Pontinus*. In *Ectreposebastes* the count is typically III, 6 with a range of 5 to 7 rays. The number of anal rays has a greater range among species of *Sebastes*. The typical counts for eastern North Pacific species of *Sebastes* are III, 6 and 7, however some species have slightly higher ray counts and *S. jordani* has III, 8 to 11 anal rays. The second of the three anal spines is usually longer than the third and heavier in juvenile and adult specimens. It should be noted that the third anal spine is late in differentiating. When first formed in larvae, it has the appearance of a soft ray. It is not ossified as a spine until the early juvenile stage; however, we have designated the third element in the anal fin as a spine in all of our counts of larvae. The change in the third anal element to a spine is gradual. Even in a cleared and stained series it is sometimes difficult to determine just when it becomes a spine; however, the total count of spines plus rays in the anal fin remains constant. For example, whether the anal count for larvae of *Sebastolobus* is given as II, 6 or III, 5, the total count remains 8. An identical problem with regard to the change-over of the third element of the anal fin from a ray to a spine is encountered in larvae of *Mugil* (Anderson 1957, 1958), and striped bass, *Morone saxatilis* (Mansueti 1958). The anterior two spines of the anal fin are supported in secondary association by a single massive, elongated pterygiophore, possibly the product of the fusion of the first two; the remaining anal spine and the anal rays are each supported by a pterygiophore and are in secondary association with the following pterygiophore (except the last ray). The pterygiophore count is two less than the total count of anal spines and rays.

The number of dorsal fin spines is a particularly useful character (Table 2). The commonest count is XII, found in *Scorpaena*, *Pontinus*, *Helicolenus*, *Trachyscorpia*, and *Ectreposebastes*. Species of *Sebastes* in the eastern North Pacific normally have XIII dorsal spines, as does *Scorpaenodes*. North Atlantic species of *Sebastes* have XIV to XVI dorsal spines, whereas *Sebastolobus* has XV to XVII. The number of dorsal soft rays is usually 9 (8 to 10) in *Sebastolobus*, *Trachyscorpia*, *Scorpaena*, *Pontinus*, *Ectreposebastes*, and *Scorpaenodes*, 11 to 13 in *Helicolenus*, and 11 to 16 in *Sebastes*. The total number of dorsal fin rays and spines is 20 to 22 in *Pontinus*, *Trachyscorpia*, and *Scorpaena*, 21 or 22 in *Ectreposebastes*, 22 to 24 in *Scorpaenodes*, 23 to 25 in *Sebastolobus*, and 24 to 31 in *Sebastes*.

The last spine in the dorsal fin of all the above scorpaenids appears first as a soft-ray and later ossifies as a spine, just as in the third spine of the anal fin. The anterior two spines of the dorsal fin are supported in secondary association by a single wide (fused) pterygiophore. In eastern Pacific scorpaenids this pterygiophore lies between neural spines two and three and is always accompanied in this space by a second pterygiophore, which carries a single spine (the third). The succeeding several pterygiophores alternate one on one with neural spines. The first and second neural spines lie close together and often point forward, in contrast to the divergent angle between neural spines two and three necessary to accommodate the anterior two pterygiophores. In several genera a single, short predorsal bone was observed immediately before the first neural spine; this bone is more readily seen on cleared and stained specimens than on radiographs.

The number of principle caudal rays (those supported by hypurals and the parhypural according to our definition) in most scorpaenid fishes is 8 + 7 = 15. The number of branched rays is either 6 + 6 (*Sebastes, Ectreposebastes*) or 6 + 5 (*Sebastolobus, Helicolenus, Scorpaenodes, Scorpaena, Pontinus*). Hence in these scorpaenid genera there are two unbranched principal rays associated with the upper lobe of the caudal fin, and either one or two associated with the lower lobe—one unbranched if the branched ray count of the lower lobe is six, two unbranched if the branched ray count is five. The principal rays of both lobes of the caudal fin are supported exclusively by hypural bones (we include the parhypural as a hypural). The primitive condition, which we have observed in *Ectreposebastes imus*, is the retention of three superior and three inferior hypurals (including the parhypural). Among the genera included in this guide, *Scorpaenodes* and *Pontinus* retain the primitive complement of three superior hypurals, but have the inferior complement reduced to two. In the other four genera there are two superior and two inferior hypurals. The primitive complement of three epurals is retained by all scorpaenids studied. Only one pair of uroneurals was observed on specimens examined. The neural spine on the vertebral centra immediately anterior to the ural is markedly reduced or lacking. The haemal spine on this vertebra is autogenous, as is the haemal spine on the vertebra immediately anteriad.

Since changes in body shape during larval development are illustrated and are emphasized in the descriptions, we will discuss them only briefly here. Newly hatched larvae of all scorpaenids studied are more slender, often markedly more slender, than are later larval stages. Larvae of *Sebastes* and *Helicolenus* are usually more slender in later larval stages than are those of the other genera. The eastern Pacific *Sebastes* with the slenderest body is *S. jordani*; in postflexion larvae the average relative body depth is less than 25% standard length (range of 22 to 26%). Relative body depth for postflexion larvae of other species ranges from 30 to 37%. Average relative body depth for postflexion specimens in the other genera is as follows: *Sebastolobus*, 35 and 41% for its two species; *Scorpaenodes*, 39%; *Scorpaena*, 38 to 40% for two species; *Pontinus*, 39 and 42% for two species; and *Ectreposebastes* up to 55%.

A knowledge of the sizes at initiation of major developmental events such as hatching, notochord flexion, and transformation aids in identifying scorpaenid larvae. There is a major dichotomy between *Sebastes* and the other genera in the size at hatching—*Sebastes* hatches at 3.8 to 7.5 mm body length and the other genera hatch at 1.8 to 2.8 mm (Table 4). *Sebastes* larvae are also longer at notochord flexion (6 to 12 mm) than the tropical genera *Scorpaenodes, Scorpaena, Pontinus*, and *Ectreposebastes* (4 to 6 mm) and the other temperate-boreal genera, *Sebastolobus* and *Helicolenus*, are intermediate (6 to 8 mm). Size at transformation from larva to pelagic juvenile is highly variable among genera and species of scorpaenids (Table 4).

Also essential for identification of scorpaenid larvae is the locality of collection. Three of the seven genera dealt with here are cold-water forms, temperate to subarctic in distribution (*Sebastes, Sebastolobus*, and *Helicolenus*) and the other four genera are tropical to subtropical. *Trachyscorpia* will probably be shown to occur only in the deep coastal waters of the southeast Pacific. The single known specimen was taken from 580 to 600 m (Chirichigno 1974) and listed as *Trachyscorpia* sp.

Over much of the California Current (CalCOFI) area, the genera that commonly cooccur are *Sebastes* and *Sebastolobus*. Although adults of *Sebastolobus* have been taken as far south as Cape San Lucas, *Sebastolobus* larvae are seldom taken south of California (Moser 1974). Larvae of some species of *Sebastes* (e.g., *S. macdonaldi*) are distributed primarily off Baja California (Moser 1972), but larvae of most species of *Sebastes* have a more northern distribution.

In the area covered on EASTROPAC and STOR cruises, between lat. 20°N and lat. 20°S, the larvae commonly taken are those of *Pontinus* and *Scorpaenodes*, with larvae of *Scorpaena* collected occasionally and larvae of *Ectreposebastes* found in equatorial waters as far offshore as long. 126°W. To the south of the EASTROPAC area, three temperate genera (*Helicolenus*, *Sebastes*, and *Trachyscorpia*) occur. Larvae of *Scorpaena guttata* are occasionally taken off southern California and occur along Baja California south to Magdalena Bay, hence cooccur commonly with *Sebastes* larvae. Lar-

Table 4. Length (mm) at hatching, notochord flexion, transformation into pelagic juveniles, and known lengths of pelagic juveniles of scorpaenid fishes included in this guide.

Species	Length at hatching or birth	Length at flexion	Length at transformation	Length of pelagic juveniles
Sebastes paucispinis	4.6	7.2- 9.7	15	15-34
macdonaldi	4.0-5.0	7.7- 9.0	15	15-44
jordani	5.4	8.0-10.0	27-30	30-63
levis	5.0	7.6-10.4	19	19-58
cortezi	4.1	7.0- 8.3	ca 17	-
Gulf Type A	4.2	7.0- 7.6	-	-
capensis	3.8	6.2- 7.0	20	-
marinus	6.7-7.2	8.5-11.8	ca 24	24-52
viviparus	5.4-5.8	7.8-10.6	-	-
fasciatus	5.8	8.5-10.0	-	-
Sebastolobus alascanus	2.6	6.0- 7.3	14-20	20-27
altivelis	2.6	6.0- 7.3	14-20	20-56
Helicolenus dactylopterus	<2.8	6.0- 7.9	-	-
Scorpaenodes xyris	1.8	4.0- 5.4	11-14	-
Scorpaena guttata	1.9-2.0	4.5- 5.7	-	-
Type A	<2.2	4.0- 5.5	-	-
Pontinus Type A	<2.3	4.1- 4.6	ca 15	15-27
Type B	-	<5.0- 5.5	ca 10	10-23
Ectreposebastes imus	<2.8	5.5	ca 28	-

vae of *Pontinus* and *Scorpaenodes* have only occasionally been taken off Baja California and as far north as the vicinity of Cedros Island. The larvae of four genera may cooccur in the Gulf of California—*Scorpaena, Scorpaenodes, Pontinus*, and *Sebastes*. Larvae of *Sebastes* and *Scorpaena* are taken commonly in the upper and middle Gulf, whereas larvae of *Pontinus* and *Scorpaenodes* are taken in the middle and lower Gulf; however, there is a broad area of overlap of the four genera in the Gulf.

Larvae of scorpaenids are commonly taken at considerable distance from shore. In the CalCOFI area, larvae are taken as far offshore as 500 km, and on EASTROPAC cruises even further offshore. Scorpaenid larvae that are taken at considerable distances offshore often belong to species that have an extended pelagic juvenile stage. A prime example is *Sebastolobus altivelis*, which spend about 20 mo in the pelagic environment from spawning to settling and attain a length of up to 56 mm as pelagic juveniles (Moser 1974). Another example is *Pontinus* Type A, the common form in the EASTROPAC area. The larvae grow to about 15 mm before transforming to pelagic juveniles, which then attain lengths up to 27.4 mm. There apparently is a large size range over which juveniles of *Pontinus* Type A become demersal, since bottom-caught specimens as small as 17.2 mm are present in collections. This may be related to the extensive offshore distribution observed for this scorpaenid, with nearshore individuals settling out first.

KEYS TO LARVAE OF EASTERN PACIFIC SCORPAENID GENERA

The most obvious feature of the larval period of marine fishes is change. Changes in form and pigmentation from hatching to transformation into the juvenile stage range from substantial to spectacular. Because of this it is impossible to write a dichotomous key that would allow identification of a species or genus of scorpaenid during all phases of its early life history. To overcome this we have constructed two keys, one for larvae which have not undergone notochord flexion and have not formed median fins and the other for larvae which have completed notochord flexion. The characters used in these keys are summarized in the preceding section and discussed in detail in the generic and species accounts. Since larvae of the eastern Pacific species of *Helicolenus* and *Trachyscorpia* were not available to us we have omitted these genera from the keys.

Key to Early Preflexion Larvae of Eastern Pacific Scorpaenid Genera[2]

1a. Melanophores on tail portion of body restricted to two large opposing blotches on dorsal and ventral margins, sometimes expanded to a solid band . . . . *Sebastolobus*

1b. Melanophores on tail along ventral midline only, or along dorsal and ventral midline, but each series contains a number of discrete melanophores 2

2a. Series of both dorsal and ventral margin melanophores developed on tail . . . . *Sebastes* (some spp.)

2b. Only ventral margin melanophores series on tail 3

3a. Melanistic shield of pigment covering dorsolateral surface of gut 4

3b. No melanistic shield covering dorsolateral surface of gut; pigment restricted to deeply embedded blotch 5

4a. Larvae 2.0 to 3.0 mm at hatching, 24 myomeres, voluminous finfold . . . . . . *Scorpaena*

4b. Larvae 4.0 to 6.0 mm at hatching, 26 or 27 myomeres, moderate finfold . . .*Sebastes* (some spp.)

5a. Melanophores on pectoral fins restricted to distal margin of fin . . . .*Scorpaenodes*

5b. Melanophores on pectoral fins distributed over entire blade of fin 6

6a. Depth of pectoral fin base 18 to 22% of body length . . . . *Ectreposebastes*

6b. Depth of pectoral fin base 15 to 16% of body length . . . . *Pontinus*

Key to Postflexion Larvae of Eastern Pacific Scorpaenid Genera[3]

1a. Parietal ridge bifurcate posteriorly, with posterior (nuchal) spine large 2

1b. Parietal ridge ending in single spine (parietal) or if two spines are present the second (nuchal) is small and positioned basally . . . 3

2a. Myomeres, 29-31; dorsal spines, XIV-XVII . . . . *Sebastolobus*

2b. Myomeres, 24 or 25; dorsal spines, XIII . . . . *Scorpaenodes*

3a. Myomeres, 26 or 27; dorsal spines XIII . . . *Sebastes*

3b. Myomeres, 24; dorsal spines, XII 4

4a. Depth of pectoral fin base, 19 to 22% of body length . . . . *Ectreposebastes*

4b. Depth of pectoral fin base 8 to 18% of body length 5

5a. Pectoral fins wing-shaped . . . . *Pontinus*

5b. Pectoral fins with rounded posterior margin . . . . *Scorpaena*

DESCRIPTION OF LIFE HISTORY SERIES

Of the 19 life history series included in this guide, 11 have not appeared previously in the literature or have appeared as fragmentary accounts. These are *Sebastes jordani, S. levis, S. cortezi, S.* sp. (Gulf of California,

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[2] Not included is *Helicolenus* from the southeastern Pacific which probably would key to couplet 4a based on the Atlantic species and *Trachyscorpia* which might key to 1a.

[3] *Trachyscorpia* probably would key to couplet 1a and *Helicolenus* to 5b.

Type A), *S. capensis*(?), *Scorpaenodes xyris, Scorpaena guttata, Scorpaena* Type A, *Pontinus* Type A, *Pontinus* Type B, and *Ectreposebastes imus.*

For each genus there is a summary of the literature and a section in which the distinguishing features of the larvae and early juveniles are summarized and compared with related genera. Our format for the species descriptions consists of a literature summary, a section entitled distinguishing features which contains the body of the description, and a description on distribution. Where there was adequate material, new descriptions are given in more detail than are those which have appeared in the literature previously. Morphometric tables and illustrations of developmental stages are included for all species. Meristic tables were prepared for only eight of the series: *Sebastes paucispinis, S. macdonaldi, S. jordani, Sebastolobus altivelis, S. alascanus, Scorpaenodes xyris, Pontinus* Type A, and *Pontinus* Type B. For the others, there were either too few specimens to sacrifice for staining or most of the specimens were leached of calcium and would not stain. Where there is no meristic table, data on fin counts are given in the distinguishing features section.

Sebastes Cuvier

Literature.—Larvae of the genus *Sebastes* are the best known of all scorpaenid genera although descriptions of only a few species have been published. Planktonic larval stages of the North Atlantic redfish, *Sebastes marinus*, were first described and illustrated by Collett (1880). This was followed by other descriptions and illustrations of intraovarian stages (Ryder 1886; Williamson 1911; Goodchild 1924; Lüling 1951; Templeman and Sandeman 1959) and planktonic stages (Dannevig 1919; Jensen 1922; Bigelow and Welsh 1925; Einarsson 1960; Tåning 1961) of that species. The taxonomy of North Atlantic *Sebastes* has long been in a state of confusion and it is likely that some of the early larval descriptions are referable to species other than *S. marinus.* Templeman and Sandeman (1959) reviewed these papers and attempted to correct the mistakes of the earlier workers. In the papers by Einarsson (1960) and Tåning (1961), the larvae of the smaller North Atlantic species, *Sebastes viviparus*, were described, illustrated, and compared with those of *S. marinus.*

Eigenmann (1892) was the first to describe the intraovarian larvae of a species of *Sebastes* from the North Pacific, *S. rubrivinctus*, and this was followed by descriptions and illustrations of intraovarian larvae of other northeastern Pacific species (Wales 1952; Morris 1956; DeLacy et al. 1964; Ahlstrom 1965; Moser 1967a, 1972; Waldron 1968; Efremenko and Lisovenko 1970; Westrheim 1975). Complete planktonic larval series of only 2 of the 65 northeastern Pacific species of *Sebastes, S. paucispinis* and *S. macdonaldi*, have been described and illustrated (Moser 1967a, 1972).

Larvae of the less speciose sebastine fauna off Japan have been described by a number of investigators. Fujita (1957, 1958) raised two species, *S. pachycephalus nigricans* and *S. oblongus*, in aquaria up to the stage of fin formation. Shiokawa and Tsukahara (1961) raised *S. pachycephalus pachycephalus* from egg to juvenile, the only time that a species of *Sebastes* has been raised through transformation. Planktonic larval series of two other Japanese species, *S. hubbsi* and *S. inermis*, have been described by Uchida et al. (1958) and Harada (1962), respectively. Takai and Fukunaga (1971) described the larval development of *S. longispinis*, and recently Sasaki (1974) has described preextrusion larvae of *S. schlegeli, S. steindachneri*, and *S. taczanowskii.*

Distinguishing features.—Despite the large species complement and resulting variety in larval form and pigmentation, there is a group of characters that allow *Sebastes* larvae to be distinguished from those of the other eastern Pacific genera.

In the earliest stages of larval development, there is a marked dichotomy in size between *Sebastes* and the other genera. At birth, *Sebastes* larvae are 3.8 to 7.5 mm long, have utilized all or most of their yolk, and have well-developed eyes and jaws. Where it is known, embryonic development of the other eastern Pacific genera occurs in floating egg masses and, at hatching, the larvae are 2.0 to 3.0 mm long, have large elliptical yolk sacs, poorly developed eyes and jaws, and a voluminous finfold that has an inflated appearance. Development is more advanced in relation to body length in these genera compared with *Sebastes*. For example, the size at initiation of notochord flexion ranges from 6.2 to 8.5 mm (mean of 7.5 ± 0.72 SD) for 10 species of *Sebastes* studied and at completion of flexion ranges from 7.0 to 11.8 mm (mean of 9.5 ± 1.39). Comparative sizes for the other genera are 4.0 to 6.0 mm (mean of 4.8 ± 0.97) at initiation of flexion and 4.5 to 7.9 mm (mean of 6.1 ± 1.32) at completion of flexion.

The extent and pattern of melanistic pigmentation is useful in distinguishing *Sebastes* larvae from those of other eastern Pacific genera. Intraovarian embryos develop a shield of melanophores over the dorsolateral surface of the gut and a series of melanophores along the ventral midline of the tail. Almost half of the known species also develop a series of melanophores along the dorsal midline of the tail before hatching. Melanophores may be added to the tail series after hatching, but the length, anteroposterior position, and number of constituent melanophores of these rows are usually stabilized at the completion of yolk absorption (Table 5). This combination of characters may be diagnostic for a particular species but, usually, species identification requires supplementary characters such as the pattern of melanophores on the pectoral fins and the presence or absence of melanophores on the lower jaw, brain lobes, and nape.

Larvae of *Sebastolobus* can be separated from *Sebastes* on the basis of the tail pigment described above. Early *Sebastolobus* larvae have two large melanistic blotches midway along the tail, which disap-

Table 5. Mean number and range of midline melanophores on tail portion of body of 33 species of *Sebastes*. All larvae were collected from identified pregnant females.

Species of *Sebastes*	Number of specimens examined	Ventral row		Dorsal row	
		$\bar{x}$	range	$\bar{x}$	range
melanostomus	27	8	4-11	0	0
macdonaldi	60	8	6-14	0	0
paucispinis	20	9	6-14	0	0
flavidus	20	10	8-12	0	0
ensifer	20	11	8-17	0	0
miniatus	40	11	8-18	0	0
eos	20	12	8-14	0	0
wilsoni	20	12	9-15	0	0
rosaceus	20	12	8-14	0	0
chlorostictus	20	13	11-14	0	0
rosenblatti	14	14	11-16	0	0
constellatus	20	14	11-17	0	0
serranoides	3	14	12-15	0	0
elongatus	20	17	12-19	0	0
diploproa	20	17	13-20	0	0
levis	20	17	13-22	0	0
brevispinis	20	18	15-23	0	0
serriceps	27	19	15-24	0	0
goodei	11	20	18-24	0	0
umbrosus	20	22	17-29	0	0
rufus	20	9	5-13	1	0-3
ovalis	20	12	10-15	15	12-18
marinus	18	18	11-24	13	8-21
jordani	18	24	21-27	19	13-28
hopkinsi	20	26	22-31	13	9-18
dallii	20	29	25-34	12	8-17
caurinus	20	42	35-58	14	9-18
saxicola	20	43	34-55	10	7-16
gilli	20	46	32-69	8	3-13
semicinctus	20	50	40-63	20	15-23
auriculatus	20	52	39-63	25	15-31
carnatus	20	55	49-63	16	11-23
maliger	20	63	54-69	13	8-19

pear in larvae 5.0 to 6.5 mm long. The warm-water genera, *Ectreposebastes, Pontinus, Scorpaena,* and *Scorpaenodes*, develop a row of about a dozen melanophores on the ventral midline of the tail in very small larvae but these are lost before the completion of notochord flexion. The dorsal midline row that forms on some species of *Sebastes* never appears on the larvae of these genera.

Late-stage larvae of *Sebastes* can be differentiated from those of other eastern Pacific genera on the basis of meristic characters. Eastern Pacific species, with a single exception, normally have 26 vertebrae and 13 spinous dorsal rays. The exception, *S. polyspinis*, has 28 vertebrae and 14 spines. *Sebastolobus* has higher counts (29 to 31 vertebrae and 15 to 17 dorsal spines) and the warm-water genera have lower counts (24 vertebrae and 12 dorsal spines). The only departure from this generalization is *Scorpaenodes* which, like *Sebastes*, has 13 dorsal spines.

Of the 69 known eastern Pacific species, complete developmental series, from newborn larvae to juvenile, are described only for *S. paucispinis* (Moser 1967a) and *S. macdonaldi* (Moser 1972), however, intraovarian and newborn larvae have been described and/or illustrated for a total of 39 eastern Pacific species. This paper contains illustrated descriptions of *S. paucispinis, S. macdonaldi, S. jordani, S. levis,* and two larval forms from the Gulf of California. Also presented are illustrations of pre- or postextrusion larvae of 23 other eastern Pacific species (Figs. 1-4). For comparative purposes, brief illustrated descriptions of *Sebastes* larvae from other regions are also given. These include eight Japanese species, a larval form from off Chile (probably *S. capensis*), and three species from the North Atlantic. Research on the larvae of the latter group is problematic because of the taxonomic confusion that surrounds the adults. Adults of the widely distributed redfish, *S. marinus*, are readily distinguished from those of *S. viviparus*, the diminutive shallow-water form of the northern European coast. The problem has been whether the deep-water "mentella" form, which cooccurs geographically with *S. marinus*, is specifically distinct from *S. marinus* and whether the "American" form is a distinct species. The work of Barsukov (1968, 1972) and Barsukov and Zakharov (1972) indicates that *S. marinus, S. mentella*, and the "American" form, *S. fasciatus*, are distinct species, making a total of at least four species in the North Atlantic. Eschmeyer's systematic review of North Atlantic redfishes (in progress, cited in Hallacher 1974) confirms this.

Sebastes paucispinis (Ayres), Figure 5

Literature.—Newly hatched larvae of the bocaccio, *S. paucispinis*, were illustrated by Morris (1956) and larval stages up to 12 mm were illustrated in Ahlstrom (1965). A complete description of the development of embryos, larvae, and juveniles was given by Moser (1967a).

Distinguishing features.—Bocaccio larvae hatch and are extruded at a length of 4.0 to 5.0 mm. Beginning at about 15 mm they undergo certain changes (e.g., diminution of parietal and preopercular spines and development of dorsal pigment saddles) that mark the beginning of the pelagic juvenile stage. Transformation into demersal juveniles occurs at 30 to 35 mm in length.

The larvae are comparatively slender. Body depth at the base of the pectoral fin averaged 20% of the body length before notochord flexion, 23% during flexion, and 30% in larvae which have completed notochord flexion (Table 6). They develop the complement of head spines typical for all species of *Sebastes* (Moser 1967a).

The most distinct morphological features of bocaccio larvae are the elongate paired fins. The pectorals begin to elongate and become aliform soon after hatching. They reach a maximum relative length of about 37% of the body length in larvae about 13 mm long. They gradually diminish in relative length during the remainder of the larval and pelagic juvenile stages and are 25% of the body length in late pelagic juveniles. Ossification of the rays begins in 6-mm larvae and the unusually small adult

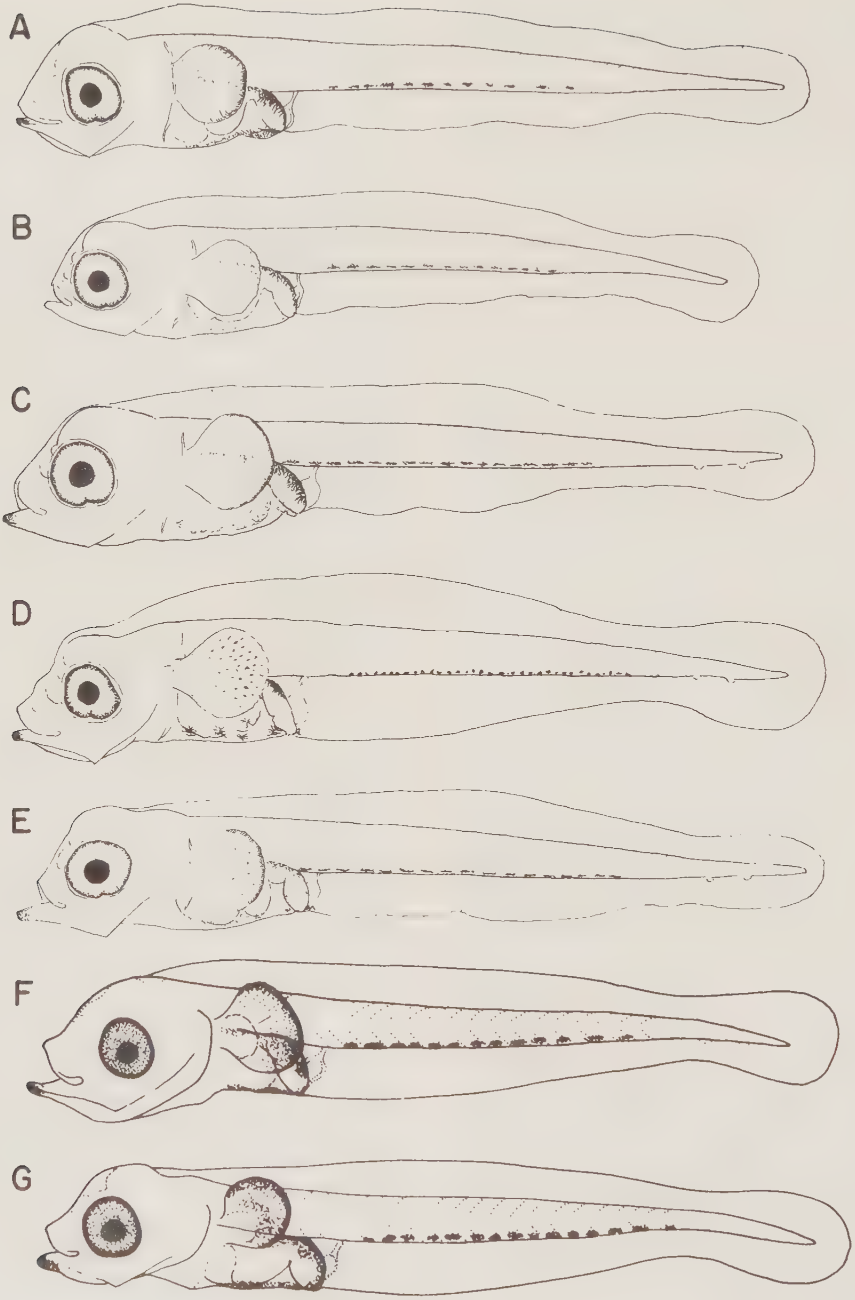

Figure 1.—Larvae of *Sebastes* (subgenus *Sebastomus*) removed from pregnant females and cultured to the point of yolk exhaustion. A. *S. constellatus*, 4.2 mm; B. *S. rosaceus*, 3.9 mm; C. *S. ensifer*, 4.2 mm; D. *S. umbrosus*, 4.2 mm; E. *S. chlorostictus*, 4.2 mm; F. *S. rosenblatti*, 4.6 mm; G. *S. eos*, 4.4 mm.

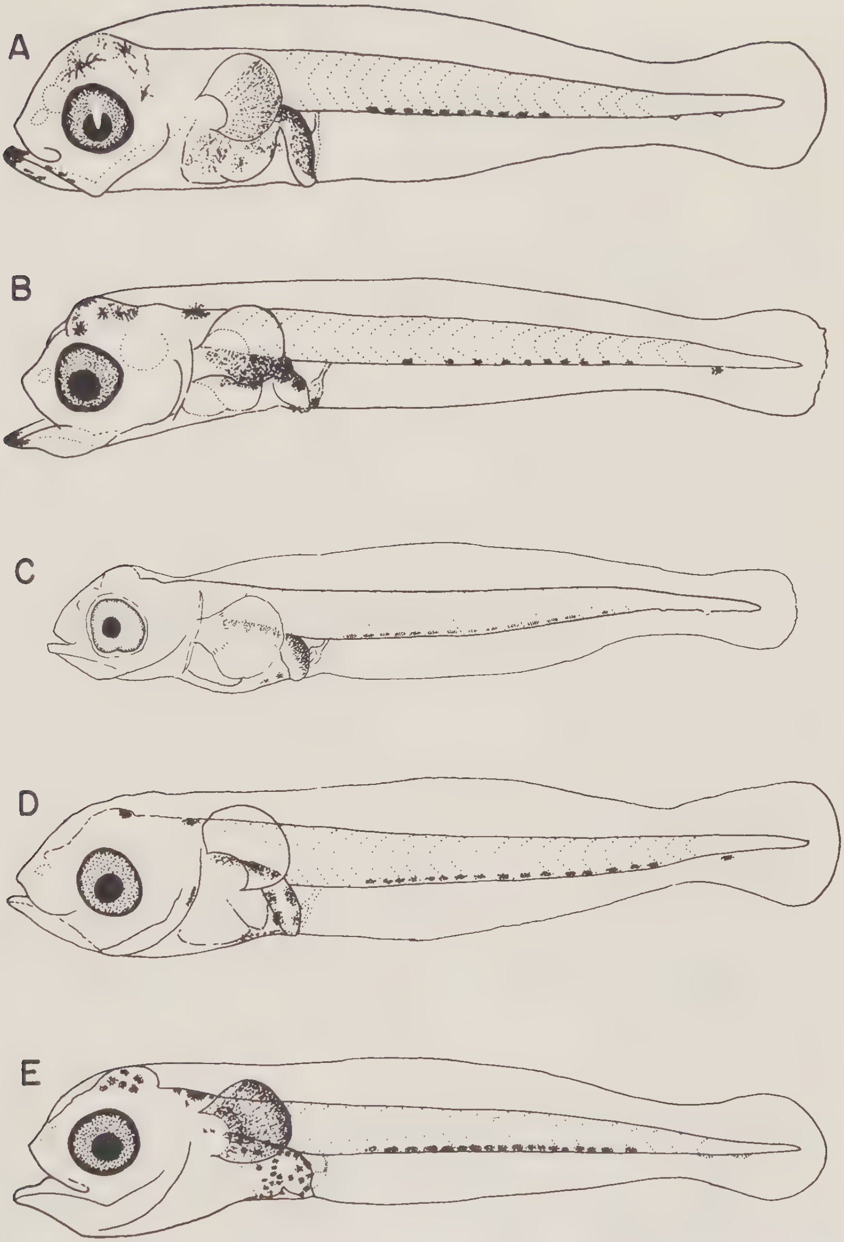

Figure 2.—Larvae of *Sebastes* at stage of yolk exhaustion. A. *S. melanostomus*, 4.4 mm; B. *S. miniatus*, 4.3 mm; C. *S. elongatus*, 4.9 mm; D. *S. serriceps*, 4.8 mm; E. *S. goodei*, 5.8 mm.

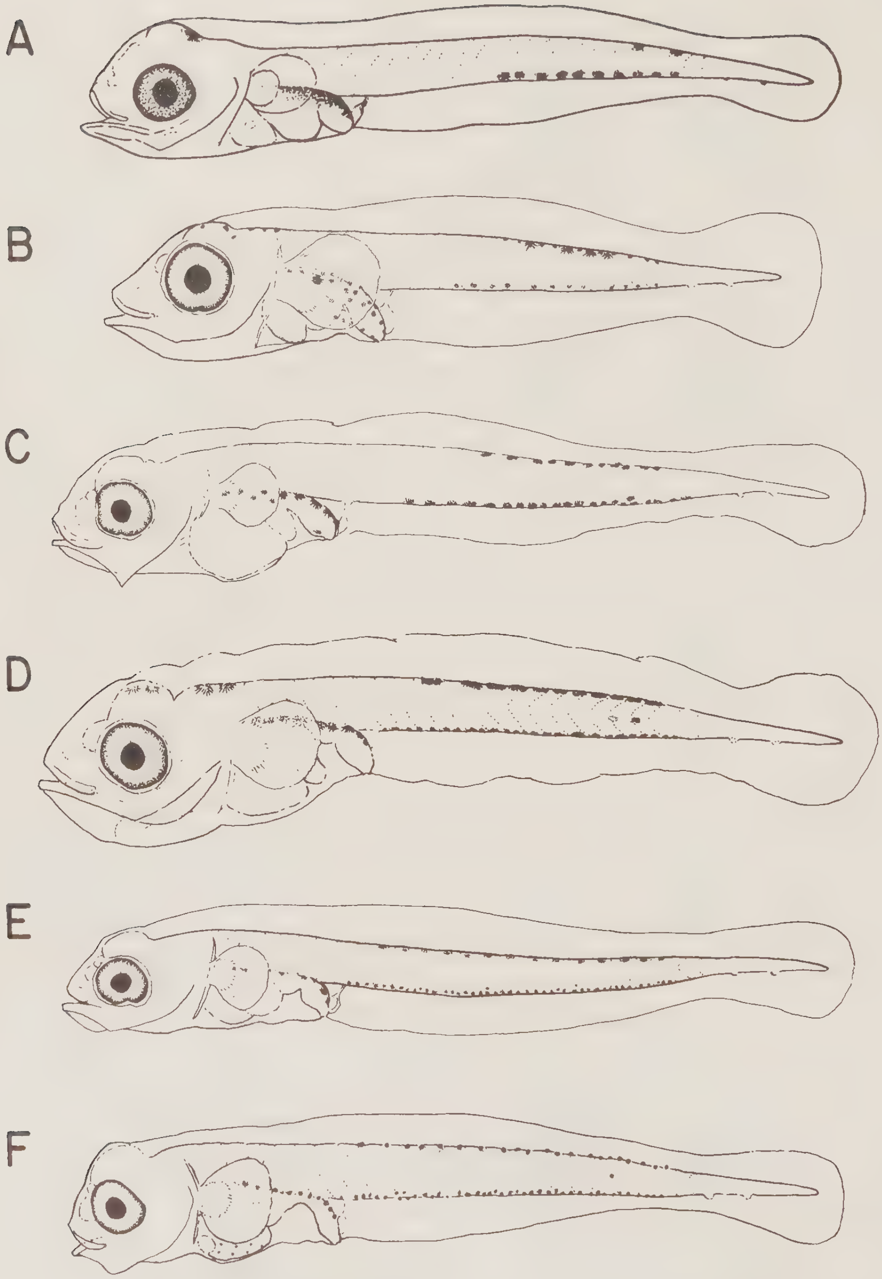

Figure 3.—Larvae of Sebastes at stage of yolk exhaustion. A. *S. rufus*, 5.3 mm; B. *S. ovalis*, 4.5 mm; C. *S. hopkinsi*, 4.7 mm; D. *S. dallii*, 4.9 mm; E. *S. semicinctus*, 5.5 mm; F. *S. carnatus*, 4.6 mm.

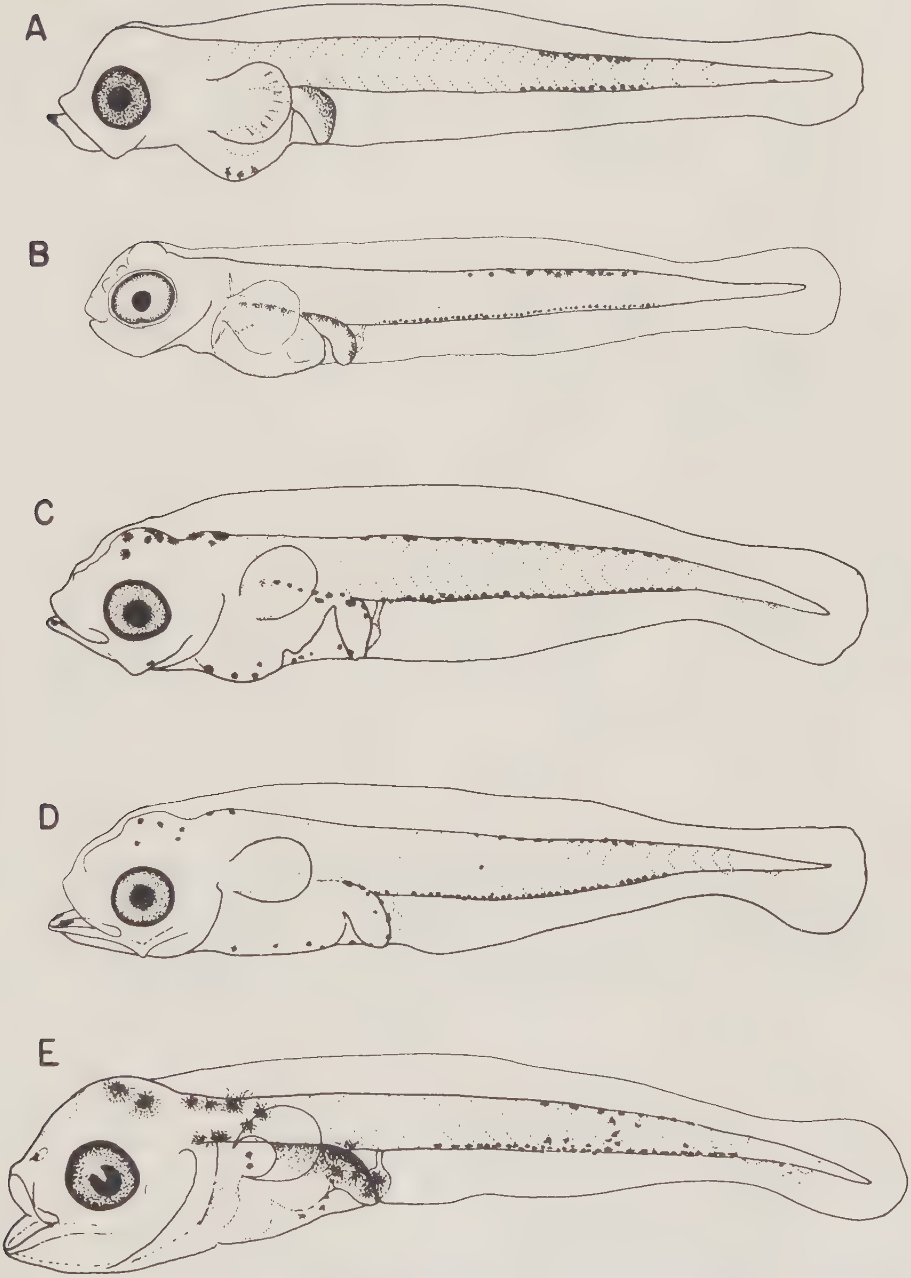

Figure 4.—Larvae of *Sebastes* at stage of yolk exhaustion. A. *S. pinniger*, 4.0 mm, redrawn from Waldron (1968); B. *S. saxicola*, 4.7 mm; C. *S. auriculatus*, 5.2 mm; D. *S. caurinus*, 5.5 mm; E. *S. gilli*, 5.2 mm. Specimens C and D supplied by C. R. Hitz.

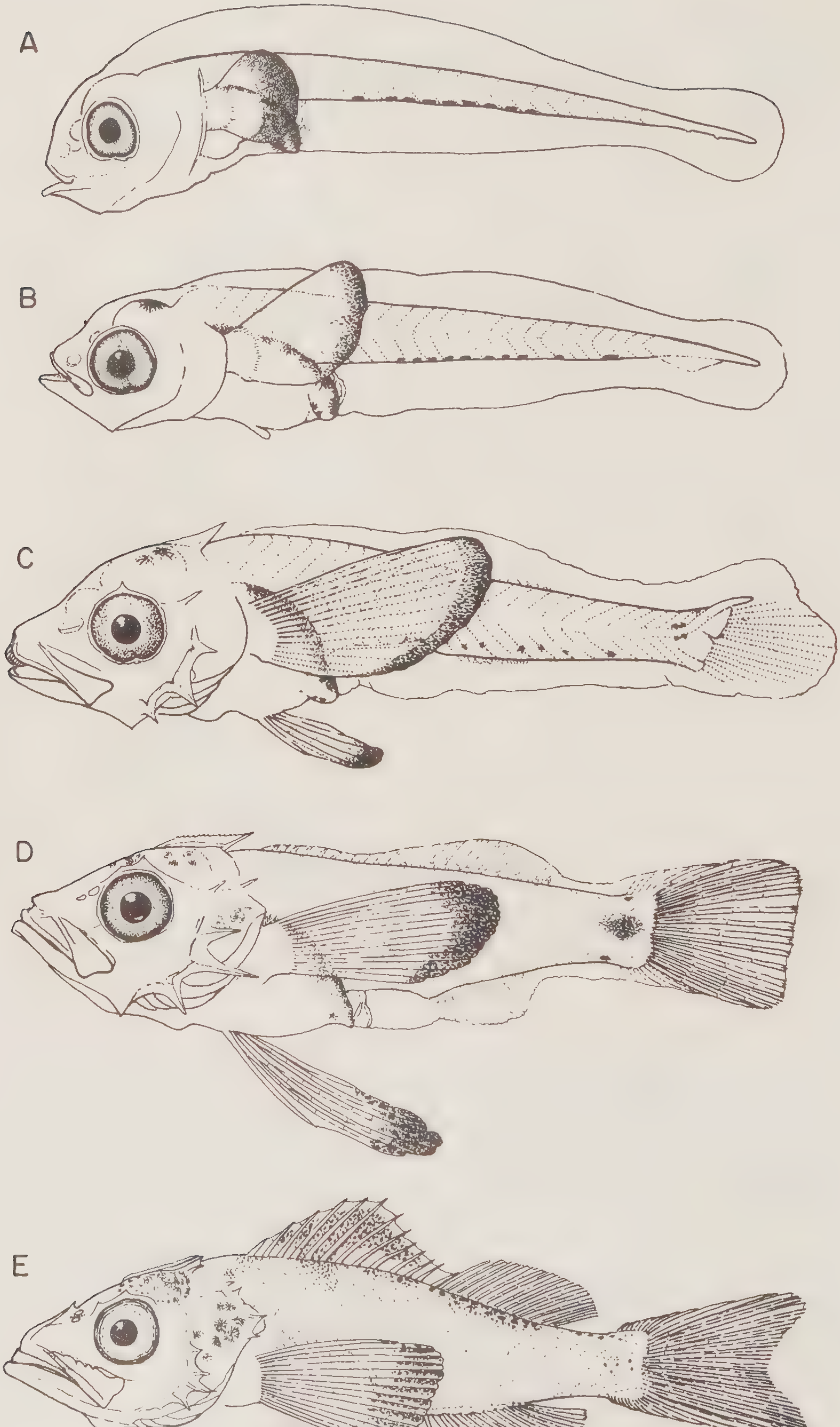

Figure 5.—Developmental series of *Sebastes paucispinis*. A. 4.7-mm larva; B. 6.1-mm larva; C. 8.7-mm larva; D. 14.0-mm larva; E. 24.2-mm pelagic juvenile.

Table 6. Measurements (mm) of Sebastes paucispinis larvae. (Specimens between dashed lines are undergoing notochord flexion.)

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-anal fin distance
4.6	1.7	1.1	0.3	0.4	0.8	0.5	0.4	-	-
4.8	1.9	1.2	0.3	0.4	0.9	0.6	0.4	-	-
5.1	2.1	1.4	0.4	0.4	1.0	0.8	0.5	0.1	-
5.8	2.5	1.7	0.4	0.5	1.2	1.2	0.5	0.2	-
6.6	2.9	1.9	0.6	0.7	1.4	1.4	0.6	0.7	-
7.2	3.2	2.1	0.6	0.6	1.7	1.8	0.7	0.9	-
7.5	3.0	2.0	0.6	0.6	1.6	1.9	0.7	0.7	-
8.2	3.5	2.4	0.7	0.8	1.8	2.3	0.7	1.1	4.9
8.8	4.2	2.7	0.9	0.8	2.1	2.4	0.8	1.4	5.2
9.7	4.8	3.1	1.0	0.9	2.3	3.0	0.8	2.5	6.0
10.3	5.3	3.8	1.2	1.2	2.9	3.7	0.8	3.3	6.3
10.5	5.7	3.9	1.3	1.2	3.1	3.6	0.8	3.7	6.9
12.0	7.0	4.5	1.4	1.4	3.5	4.4	1.0	4.7	7.9
12.7	7.1	4.6	1.5	1.5	3.7	4.6	1.0	4.6	8.1
13.7	8.2	5.0	-	1.4	4.1	5.1	1.0	5.1	9.2
14.2	8.6	5.5	1.8	1.7	4.2	4.8	1.0	4.4	9.2
15.0	9.1	5.5	1.7	1.8	4.6	5.4	1.1	5.4	9.7
24.2	15.2	8.8	2.9	2.6	6.9	8.3	1.3	5.7	-
29.4	19.0	11.3	2.9	3.0	8.1	7.4	1.7	7.3	-
*32.0	19.2	11.7	3.4	3.0	8.8	8.3	1.7	7.8	-
*34.4	20.6	11.5	3.8	3.1	9.4	8.8	2.0	7.5	22.3

*Transforming specimens.

complement of pectoral rays is present in 9-mm larvae (Table 7). The pelvic fins begin to develop in 5-mm larvae and, like the pectorals, reach a maximum relative length of 37% of the body length in 13-mm larvae.

Bocaccio larvae may be readily identified by their pigment pattern. The most striking melanistic pigment is on the posterior margins of the pectoral and pelvic fins. This pigment remains throughout the larval period and is found in juveniles up to about 70 mm. Other patches of melanophores develop above the brain, on the opercle, and at the base of the caudal fin. The number of melanophores in the ventral midline series is small compared with other species of *Sebastes*. Their number ranged from 6 to 14 with a mean of 9 for 20 larvae counted.

Distribution.—Adults of *S. paucispinis* have been taken as far south as Punta Blanca, Baja California, and as far north as Kodiak Island, although the principal distribution of the species is off California; they have been reported offshore to depths of 320 m (Miller and Lea

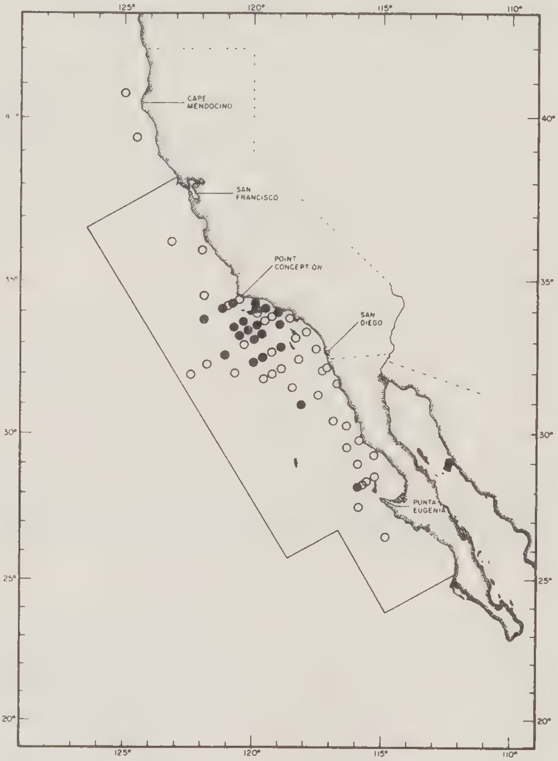

Figure 6.—Stations at which larvae of *Sebastes paucispinis* were collected by CalCOFI plankton surveys during 1953 and 1956. Solid circles indicate stations where number of larvae exceeded mean number (6.7) for all positive stations. Area of frequent occupancy is outlined (see Ahlstrom 1961 for complete grid).

Table 7. Meristics from cleared and stained larvae of Sebastes paucispinis.

Length (mm)	Principal caudal fin rays		Procurrent caudal fin rays		Branchiostegal rays		Pectoral fin rays		Hypural elements		Gill rakers (right arch)		Anal fin rays	Dorsal fin rays	Pelvic fin rays		Vertebrae
	superior	inferior	superior	inferior	left	right	left	right	superior	inferior	upper limb	lower limb			left	right	
6.6	3	3	-	-	4	4	10	10	-	-	-	3	-	-	-	I-2	-
7.2	5	5	-	-	5	5	12	12	-	-	-	6	-		I-3	I-3	-
8.8	7	7	-	1	6	6	14	14	-	-	-	7	-	-	I-4	I-4	4
9.3	7	7	-	-	7	7	15	15	-	-	2	11	-	-	I-5	I-5	22
10.3	8	7	2	3	7	7	15	15	1	2	2	12	I-7	IV-9	I-5	I-5	23
11.0	8	7	4	4	7	7	15	15	1	2	4	13	II-9	XIV-14	I-5	I-5	26
11.8	8	7	6	7	7	7	15	15	1	2	4	14	III-9	XIII-14	I-5	I-5	26
12.0	8	7	7	8	7	7	15	15	1	2	5	15	III-9	XIII-14	I-5	I-5	26
13.4	8	7	8	8	7	7	15	15	1	2	5	15	III-9	XIII-15	I-5	I-5	26
14.2	8	7	11	11	7	7	15	15	1	2	6	17	III-9	XIII-14	I-5	I-5	26

1972). Information from CalCOFI samples shows that bocaccio larvae occur as far south as Punta San Hippolito, Baja California, and seaward to about 400 km (Fig. 6). The distribution of bocaccio larvae is not known north of California since the CalCOFI sampling pattern usually is terminated at the California-Oregon border. Bocaccio larvae are present in CalCOFI samples for an 8-mo period from November to June with a peak abundance in January and February. Seasonal changes in abundance and size of larvae are shown in Table 8.

Table 8. Mean lengths (mm) of *Sebastes paucispinis* larvae collected on cruises of the California Cooperative Oceanic Fisheries Investigations during 1953 and 1956. (Standardized numbers of larvae are shown in parentheses.)

	JAN	FEB	MAR	APR	MAY	JUN	NOV	DEC
1953	5.3(88)	5.2(221)	8.2(82)	10.2(47)	13.2(5)	12.2(10)	4.0(7)	4.5(56)
1956	4.9(89)	5.4(43)	7.8(27)	8.4(19)	15.7(12)	7.9(5)	—	4.5(37)

Sebastes macdonaldi (Eigenmann and Beeson), Figure 7

Literature.—A description of the larvae and pelagic and benthic juveniles of *S. macdonaldi*, the Mexican rockfish or "coral cod," is presented in Moser (1972).

Distinguishing features.—Larvae of *S. macdonaldi* are born at a length of 4.0 to 5.0 mm. The gradual transformation into pelagic juveniles begins at about 15 mm. The pelagic juvenile phase appears to be highly protracted, since the smallest demersal juveniles known are about 60 mm in length.

Larvae of this species are relatively deep-bodied. Body depth at the base of the pectoral fins averages 23% of the body length before notochord flexion, 33% during notochord flexion, and 34% in larvae which have completed notochord flexion (Table 9). The sequence of development of the head spines is described in detail in Moser (1972).

The pectoral fins are short and compact, although they gradually increase in length during the larval period. Fin length averages 8% of the body length before notochord flexion, 13% during flexion, and 19% in larvae which have completed flexion. The fin elongates markedly in pelagic juveniles, where its average length is 31% of the body length. The sequence of ossification of the fins and bony skeleton is given in Table 10.

The most distinctive pigment is on the paired fins. The pectorals are covered solidly with melanophores in newborn larvae. When rays develop the solid pigmentation is restricted to the membranes between the rays but the overall appearance is a dark compact fin with light striations. The pelvic fins develop similar pigmentation. When the paired fins become elongate in pelagic juveniles, they retain their distinct dark pigmentation. Early larvae have a group of melanophores on the nape and an unusually low number of melanophores in the ventral tail series. In a sample of 60 newborn larvae, the number of ventral midline melanophores ranged from 6 to 14 with a median of 8. Patches of melanophores develop over the brain, on the opercle and preopercle. Late in the larval period, melanophores form lateral to the base of the dorsal fin. It is from these elongate patches that the striking pigment saddles extend ventrad in pelagic juveniles.

Table 9. Measurements (mm) of larvae and pelagic juveniles of *Sebastes macdonaldi*. (Specimens between dashed lines are undergoing notochord flexion.)

Standard length	Snout-Anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pelvic fin length	Snout-anal fin distance
4.5	1.8	1.1	0.38	0.37	0.09	0.27	-	-
4.7	1.8	1.2	0.30	0.45	1.0	0.40	-	-
5.0	1.8	1.2	0.30	0.46	1.0	0.33	-	-
5.2	2.1	1.4	0.48	0.51	1.2	0.36	-	-
5.7	2.4	1.6	0.47	0.57	1.3	0.52	-	-
5.9	2.6	1.8	0.48	0.55	1.5	0.45	-	-
6.3	2.8	1.8	0.56	0.57	1.6	0.60	0.05	-
6.7	2.9	1.9	0.56	0.63	1.7	0.61	0.04	-
6.8	3.1	1.9	0.55	0.70	1.8	0.62	0.15	-
7.0	3.3	2.1	0.75	0.70	1.9	0.60	0 12	-
7.6	3.5	2.2	0.79	0.73	2.0	0.68	0.20	-
7.7	3.8	2.7	0.82	0.84	2.3	0.90	0.33	4.2
7.9	3.8	2.7	0.80	0.90	2.5	0.93	0.25	4.2
8.2	4.2	2.9	1.1	1.0	2.5	1.1	0.52	4.8
8.5	4.7	3.2	1.2	1.0	3.0	1.3	0.80	4.9
9.0	5.0	3.2	1.1	1.0	2.8	1.2	0 65	5.4
9.2	5.3	3.4	1.1	1.1	3.1	1.4	0.89	5.4
9.5	5.2	3.6	1.3	1.2	3.1	1.5	1.1	5.6
9.7	5.4	3.5	1.2	1.2	3.2	1.6	1.1	5.8
10.0	6.2	3.7	1.2	1.3	3.5	1.8	1.2	6.4
10.3	6.3	3.8	1.4	1.3	3.5	1.7	1.2	6.5
11.2	6.8	3.8	1.4	1.3	4.0	2.1	1.5	7.0
12.0	7.7	4.5	1.4	1.5	4.2	2.4	1.8	7.7
15.0	9.4	5.8	1.7	1.9	5.2	3.5	3.1	9.7
15.4	9.3	5.8	1.7	1.8	5.5	4.0	2.9	9.6
15.9	10.0	6.5	2.1	2.0	5.2	3.6	2.8	10.1
*22.6	14.0	8.4	2.7	2.3	7.5	6.7	4.8	14.7
*27.8	18.6	10.6	3.1	2.8	8.9	8.8	6 2	19.3
*29.2	19.1	10.8	2.9	3.2	10.0	9.8	6.5	19.9
*32.7	20.7	11.8	3.2	3.6	10.1	9.7	-	20.8
*34.5	20.9	11.8	3.2	4.0	10.5	10.6	7.7	21.4
*38.8	25.0	12.8	3.2	4.0	11.7	11.2	8.3	25.6
*40.5	26.8	13.0	3.5	4.2	12.0	12.2	8.5	27.4
*44.4	30.2	14.0	3.8	4.7	13.2	13.2	9.2	31.2

*Pelagic juvenile.

Distribution.—This species has the most southerly distribution of any species of *Sebastes* in the eastern North Pacific. Adults have been taken as far north as Pt. Sur, Calif., and as far south as Morgan Bank, near Cape San Lucas, Baja California. Its abundance on the banks off southern Baja California, and in certain areas of the Gulf of California, suggests that the outer coast populations and the Gulf populations may be continuous (Moser 1972).

CalCOFI data show that larvae of this species are most abundant off central Baja California. Larval abundance declines sharply to the north of this region and larvae do not occur north of Los Angeles (Fig. 8). Larval abundance falls off less sharply to the south of Punta Eugenia; however, the CalCOFI sampling pattern does not allow exact delimitation of the southern range of *S. macdonaldi* larvae.

The larvae are present in CalCOFI samples over a 6-mo period from January to June with a peak abundance in March. Seasonal changes in abundance and size of larvae are shown in Table 11. A few larvae of this species were taken in the Gulf of California.

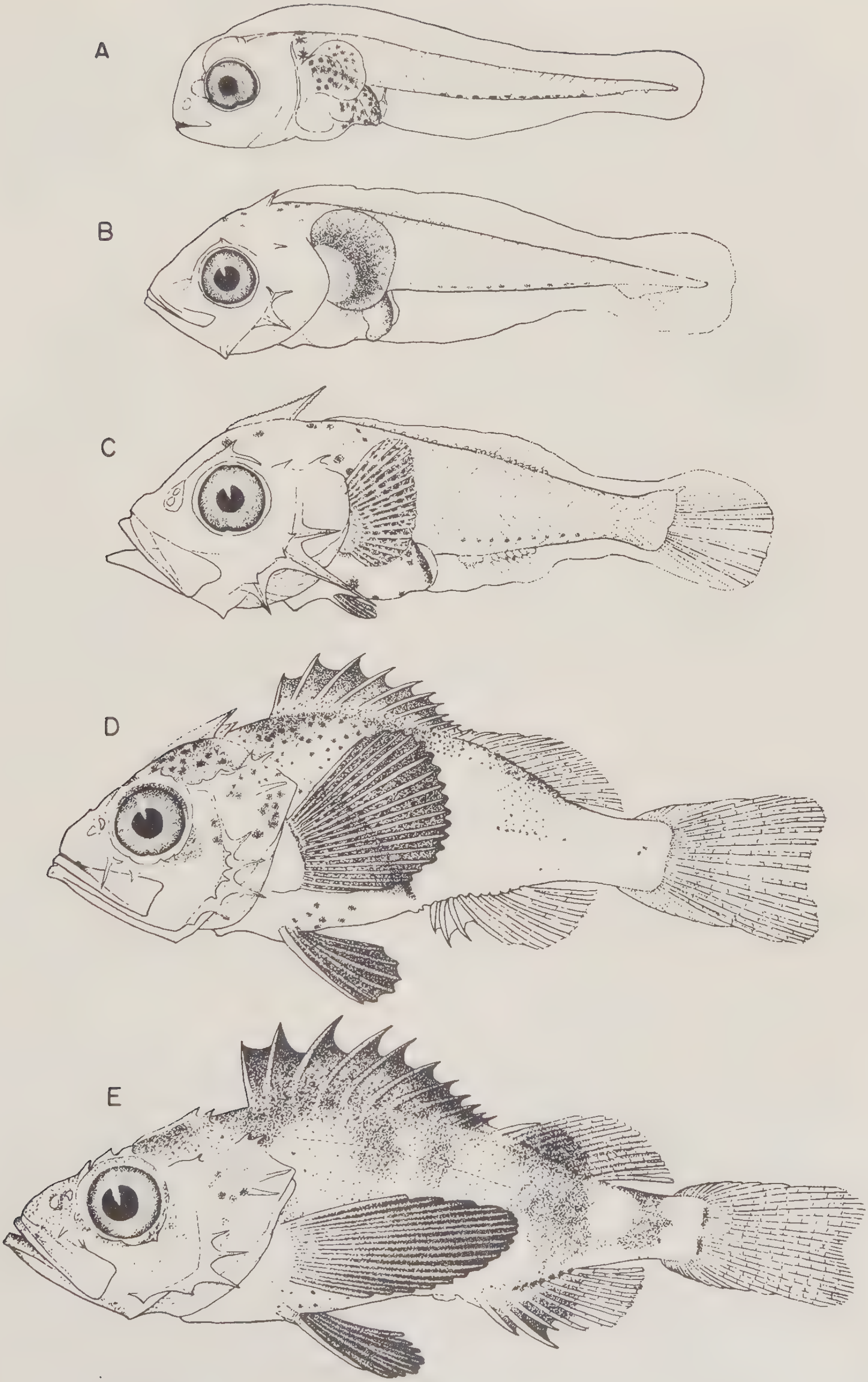

Figure 7.—Developmental series of *Sebastes macdonaldi*. A. 4.5-mm larva; B. 6.3-mm larva; C. 9.0-mm larva; D. 15.4-mm transforming specimen; E. 29.2-mm pelagic juvenile.

Table 10. Meristics from cleared and stained larvae of Sebastes macdonaldi.

Length (mm)	Principal caudal fin rays		Procurrent caudal fin rays		Branchiostegal rays		Pectoral fin rays		Hypural elements		Gill rakers (right arch)		Anal fin rays	Dorsal fin rays	Pelvic fin rays		Vertebrae
	superior	inferior	superior	inferior	left	right	left	right	superior	inferior	upper limb	lower limb			left	right	
6.3	-	-	-	-	2	2	2	2	-	-	-	-	-	-	-	-	-
6.7	-	-	-	-	3	3	3	3	-	-	-	-	-	-	-	-	-
6.8	-	-	-	-	3	3	3	-	-	-	-	4	-	-	-	-	-
7.0	3	3	-	-	4	4	6	6	-	-	-	5	-	-	-	-	-
7.1	4	3	-	-	5	5	6	6	-	-	-	6	-	-	-	-	-
7.2	3	3	-	-	5	5	-	8	-	-	-	6	-	-	-	-	-
7.7	6	6	-	-	6	6	11	11	-	-	-	9	-	-	I-0	I-0	5
7.9	4	4	-	-	5	5	9	10	-	-	-	9	-	-	-	-	3
8.2	8	7	2	2	7	7	17	17	-	-	1	12	III-4	VII-0	I-3	I-3	24
8.5	7	7	-	1	6	6	15	15	1	1	1	11	-	-	I-3	I-3	18
8.7	8	7	-	1	7	7	16	16	-	-	1	12	-	IV-0	I-3	I-3	18
9.2	8	7	2	3	7	7	19	18	2	3	3	14	-	VII-8	I-4	I-4	23
9.4	8	7	4	4	7	7	19	19	2	3	3	15	III-7	XIII-13	I-5	I-5	24
9.7	8	7	3	4	7	7	19	19	2	3	3	16	III-7	XIII-13	I-5	I-5	24
10.0	8	7	5	6	7	7	19	19	2	3	5	17	III-7	XIII-13	I-5	I-5	26
10.3	8	7	5	5	7	7	19	20	2	3	-	-	III-7	XIII-13	I-5	I-5	26
11.3	8	7	4	4	7	7	19	19	2	3	5	18	III-7	XIII-13	I-5	I-5	26
12.0	8	7	8	7	7	7	19	19	2	2	5	18	III-7	XIII-13	I-5	I-5	26
15.0	8	7	10	11	7	7	19	19	3	2	-	-	III-7	XIII-13	I-5	I-5	26
15.9	8	7	10	11	7	7	19	19	3	2	9	21	III-6	XIII-12	I-5	I-5	26
27.8	-	-	-	-	7	7	18	18	2	2	10	25	III-7	XIII-13	I-5	I-5	26

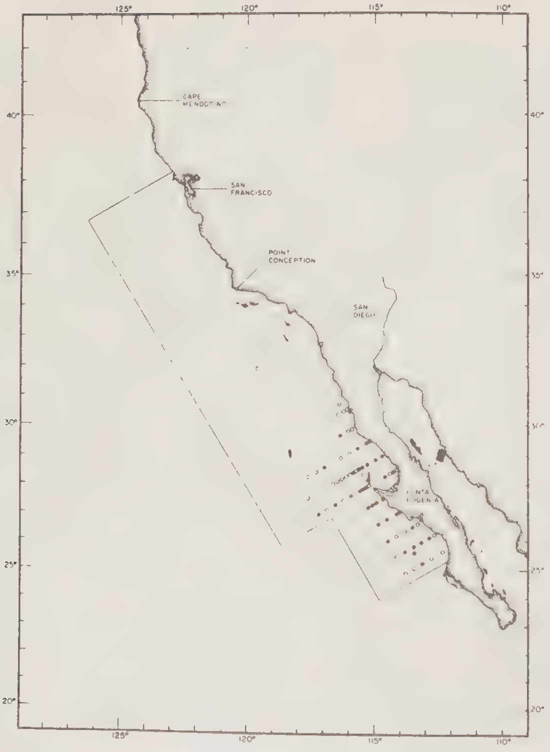

Figure 8.—Stations at which larvae of *Sebastes macdonaldi* were collected during 4 yr (1953, 1960, 1965, and 1966) of CalCOFI plankton surveys. Solid circles indicate stations where number of larvae exceeded mean number (4.8) for all positive stations. Area of frequent occupancy is outlined (see Ahlstrom 1961 for complete grid).

Table 11. Mean lengths (mm) of Sebastes macdonaldi larvae collected on cruises of the California Cooperative Oceanic Fisheries Investigations during 1953 and 1960. (Standardized numbers of larvae are shown in parentheses.)

	JAN	FEB	MAR	APR	MAY	JUN
1953	4.3 (45)	4.6 (109)	4.9 (632)	5.6 (163)	5.2 (22)	7.8 (2)
1960	4.2 (3)	4.8 (65)	5.1 (1042)	5.1 (248)	5.2 (48)	4.6 (15)

Sebastes jordani Gilbert, Figure 9

Literature.—Morris (1956) described briefly the newly extruded larvae of *S. jordani* and illustrated a 6.8-mm specimen.

Distinguishing features.—The larvae of the shortbelly rockfish, *S. jordani*, are larger at hatching than other eastern Pacific species studied to date. Morris (1956) illustrated a newly hatched *S. jordani* larva 6.8 mm in length, however, the mean for 20 measured specimens was 5.4 mm. This is 0.75 mm larger than the mean length for the next largest species listed by Morris. Newly hatched larvae of most other eastern Pacific species are between 3.8 and 5.0 mm. The 6.8-mm length of Morris' illustrated specimen is above the upper range of any eastern Pacific species known to us and is more like the lengths of newly hatched larvae of the *S. marinus* group of the Atlantic and some Japanese species. Other similarities between the larvae of *S. jordani* and the *S. marinus* group suggest that the two may be closely related. *Sebastes jordani* larvae have an extended larval period. Transformation into the pelagic juvenile stage occurs at about 27 mm and specimens in the 28- to 30-mm

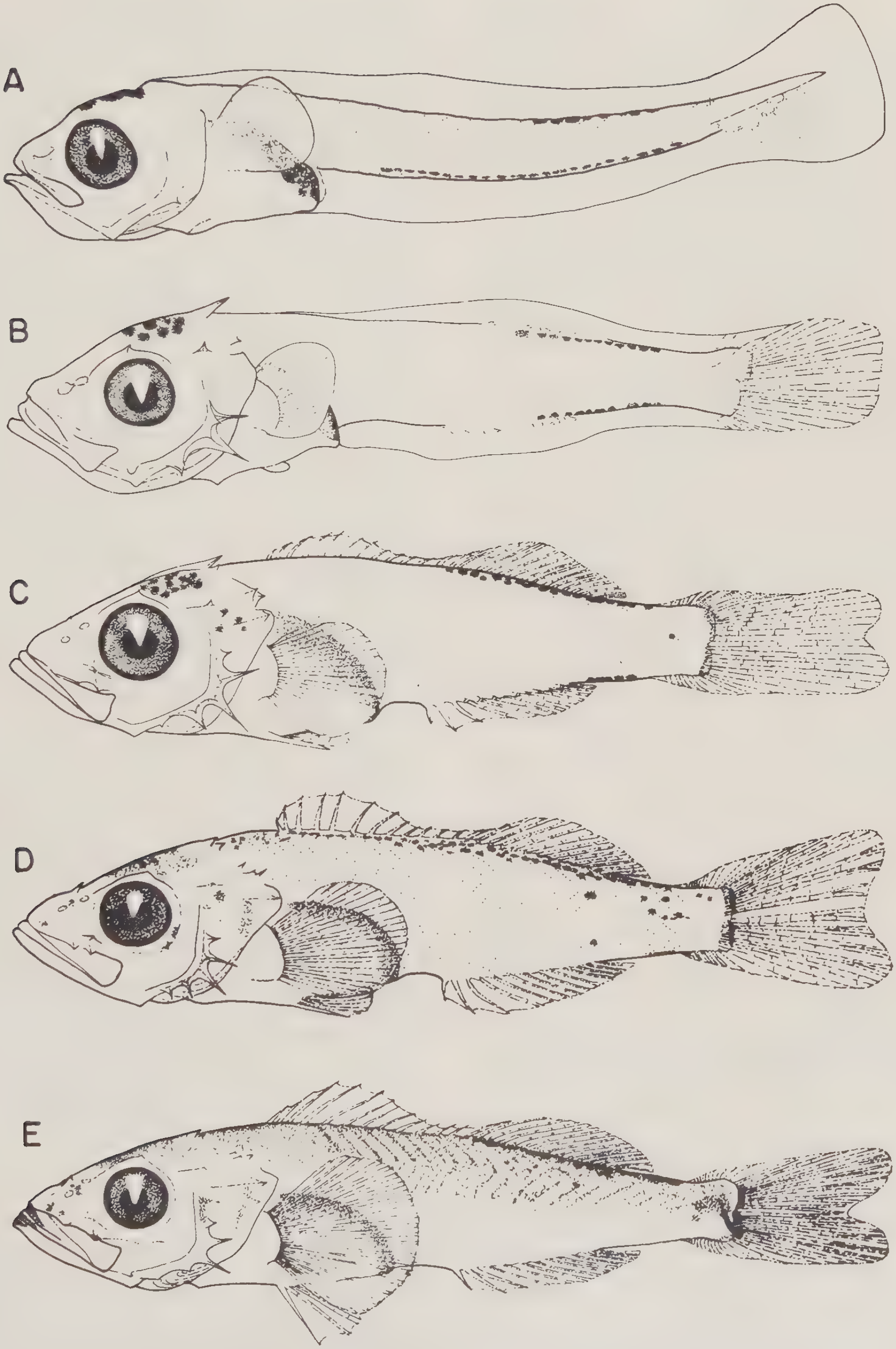

Figure 9.—Developmental series of *Sebastes jordani*. A. 7.2-mm larva; B. 10.0-mm larva; C. 15.5-mm larva; D. 21.0-mm larva; E. 29.6-mm pelagic juvenile.

size range have the morphological and pigmentary features of pelagic juveniles. This is also true for *S. marinus*. Pelagic juveniles remain in the surface waters; they appear to form schools soon after transformation and are particularly susceptible to dip netting under nightlights. Juveniles in the 30- to 50-mm size range are commonly dip netted and a 62.8-mm specimen was taken by this method (Table 12).

Larvae of *S. jordani* are the most slender of all *Sebastes* yet described. Body depth averages 17% of the body length before notochord flexion, 21% during flexion, and 23.5% following flexion. Pelagic juveniles 28 to 68 mm long appear to be slightly more slender, with a mean of 22%.

The rounded pectoral fins are the shortest of any eastern Pacific rockfish larvae yet described. Pectoral fin length averages 7% of the body length prior to notochord flexion and 8% during flexion. This percentage increases gradually following notochord flexion from 11% immediately after flexion to 20% in the largest larvae. There is only a slight increase in relative pectoral fin length during the pelagic juvenile stage, up to 22% in the largest specimen available (62.8 mm). The small pectorals in *S. jordani* and the ontogenetic changes in relative size agree closely with the condition in the larvae of the *S. marinus* group. The sequence of ossification of the pectorals and other fins is shown in Table 13.

Table 12. Measurements (mm) of larvae of Sebastes jordani. (Specimens between dashed lines are undergoing notochord flexion.)

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-anal fin distance
5.4	2.0	1.2	0.28	0.46	0.85	0.38	0.32	---	---
5.8	2.1	1.2	0.31	0.45	0.95	0.32	0.38	---	---
6.1	2.2	1.3	0.30	0.49	1.0	0.43	0.43	---	---
6.4	2.4	1.6	0.48	0.60	1.2	0.45	0.45	---	---
7.2	2.6	1.6	0.45	0.61	1.2	0.48	0.46	---	---
7.7	2.8	1.8	0.55	0.65	1.4	0.50	0.50	---	--
8.0	3.3	2.1	0.72	0.74	1.6	0.62	0.60	0.07	4.4
8.6	3.7	2.2	---	0.78	1.8	0.64	0.63	0.08	4.8
9.0	3.7	2.7	0.94	0.87	1.8	0.70	0.70	0.10	5.2
9.4	4.2	2.8	1.0	0.92	2.1	0.83	0.75	0.18	5.2
10.0	4.2	3.0	1.1	0.88	2.2	1.0	0.82	0.18	5.8
10.5	4.8	3.3	1.2	1.0	2.4	1.2	1.0	0.35	6.4
11.6	5.3	3.9	1.4	1.1	2.5	1.4	1.0	0.44	6.9
12.8	6.2	4.1	1.6	1.2	3.1	1.7	1.1	0.50	7.6
13.4	7.2	4.8	1.7	1.3	3.2	2.0	1.1	1.0	8.8
15.5	8.0	5.0	1.7	1.7	4.1	2.5	1.2	1.4	9.2
21.0	11.3	6.7	2.2	2.1	5.2	3.9	1.7	2.2	12.2
22.8	11.7	7.4	2.6	2.1	5.3	4.1	1.6	2.5	13.2
23.5	12.0	7.5	2.6	2.2	5.6	4.6	1.8	2.7	13.8
24.5	12.8	8.2	2.9	2.2	5.4	4.7	1.7	3.0	15.0
25.5	13.8	8.1	2.7	2.3	6.3	4.8	1.8	2.9	15.0
26.4	13.8	8.3	2.8	2.4	6.3	5.0	1.9	3.3	15.7
27.0	14.0	8.5	2.[illegible]	2.7	6.4	5.3	1.9	3.4	16.4
*28.4	15.0	9.5	3.2	2.6	6.4	5.4	2.0	3.3	17.2
*29.6	15.7	9.[illegible]	3.2	2.6	6.9	5.8	2.2	3.7	18.1
*30.3	16.7	10.0	3.8	2.6	6.7	6.2	2.1	3.8	19.3
*40.7	22.0	12.8	4.6	3.1		8.5	2.7	5.4	25.8
*50.7	26.5	15.0	4.8	4.2	11.2	11.0	3.3	7.5	31.5
*62.8	33.0	17.4	5.2	4.6	13.5	13.5	4.2	9.2	38.3

*Pelagic juvenile.

A character which separates adults and juveniles of *S. jordani* from all other known species of *Sebastes* is the anterior placement of the anus. In his key Phillips (1957) indicated that the distance between the anus and the first anal spine in *S. jordani* is 1.1 to 1.5 orbit diameters, whereas this distance is 0.1 to 0.8 orbit diameters in other species. This wide space between the anus and the anal fin origin is conspicuous in pelagic juveniles and is a useful character in identifying all but the smallest larvae. Snout-anus distance averages 36% of the body length in the larvae prior to notochord flexion, 42% during flexion, and 51% following flexion. In pelagic juveniles it is 54%. Comparative mean percentages for larvae of *S. paucispinis* are 41 before flexion, 45 during flexion, and 59 following flexion. For larvae of *S. macdonaldi*, the percentages are 42, 52, and 60.

The pigment pattern of early *S. jordani* larvae is similar to that of the *S. marinus* group in the Atlantic. Newborn larvae have the melanistic shield over the gut, a group of melanophores above the brain, and a series of melanophores along the dorsal and ventral midlines of the tail. The ventral row begins at the 3rd to 5th postanal myomere and extends to the 14th and 16th postanal myomere. Typically, in the anterior two-thirds of the series, the melanophores are positioned singly, but in the posterior two-thirds the melanophores are in two irregular rows along the ventral midline. For 15 specimens counted, the total number in the ventral row ranged from 21 to 27 with a mean of 23.7 ± 1.75 SD. The dorsal row is considerably shorter, beginning at the 7th to 12th postanal myomere and extending posteriad to the 14th to 16th myomere. The melanophores are bunched together in an irregular row that contains a mean of 18.9 ± 4.64 melanophores (range of 13 to 28) for 18 larvae counted.

Table 13. Meristics from cleared and stained larvae of Sebastes jordani.

Length (mm)	Principal caudal fin rays		Procurrent caudal fin rays		Branchiostegal rays		Pectoral fin rays		Hypural elements		Gill rakers (right arch)		Anal fin rays	Dorsal fin rays	Pelvic fin rays		Vertebrae
	superior	inferior	superior	inferior	left	right	left	right	superior	inferior	upper limb	lower limb			left	right	
9.4	8	7	0	1	7	7	10	10	-	-	0	11	-	-	-	-	18
10.0	8	7	0	0	7	7	13	13	-	-	1	12	-	-	-	-	20
10.5	8	7	2	2	7	7	16	16	2	3	2	15	-	-	I-3	I-3	24
11.2	8	7	0	3	7	7	16	16	2	3	2	15	-	-	I-3	I-3	27
12.5	8	7	3	4	7	7	19	19	2	2	4	18	III-6	XIII-6	I-5	I-5	27
12.8	8	7	5	5	7	7	19	19	2	2	4	19	III-11	XIII-13	I-4	I-4	27
22.0	8	7	10	12	7	7	21	21	2	2	10	26	III-11	XIII-14	I-5	I-5	27

Development of pigment pattern in later larval stages is also similar to that in the *S. marinus* group of the Atlantic. The ventral series on the tail becomes embedded and obscure; beginning at the anterior end of the series this process gradually proceeds posteriad until, in 15-mm larvae, only those melanophores posterior to the anal fin are visible. With further development, these too are obscured. The dorsal series follows an opposite course. Melanophores are added anteriorly to form streaks on either side of the developing dorsal fin. Melanophores are also added posteriorly so that the dorsum is pigmented from head to caudal fin. Melanophores begin to appear on the side of the tail just anterior to the caudal fin in larvae of about 15 mm in length. Also, the posterior margins of the hypural elements become outlined with embedded pigment.

At transformation, which begins in specimens about 27 mm long, the upper half of the body above the lateral line begins to be covered with fine melanophores. These melanophores are more concentrated at the myosepta and accent them. The streaks along the soft dorsal fin and the streak above the caudal peduncle are darker than on the more anterior region of the dorsum. In 40-mm pelagic juveniles, the general body pigmentation begins to extend below the lateral line, but even in later juveniles and in adults, the ventral region of the body is paler than the dorsal half. The pectoral and pelvic fins develop no melanistic pigmentation in larvae or pelagic juveniles.

Distribution.—According to Miller and Lea (1972), *S. jordani* ranges from British Columbia south to Cape Colnett, Baja California (about lat. 31°N). A 45.2-mm juvenile (SIO 71-120) dip netted off west San Benito Island (lat. 28°18.0'N, long. 115°34.25'W) extends the range of this species about 270 km south. The distribution of *S. jordani* larvae in the CalCOFI sampling area during 1966 is shown in Figure 10. The sampling area obviously stops short of the northward extent of spawning, however, it shows the southern extent of larval occurrence to be just south of the border with Mexico (CalCOFI Line 100). Another obvious feature is the coastal nature of *S. jordani* distribution. All larvae were taken in the shoreward region of the sampling grid and the largest individual catches were made on stations next to the coast.

Frequency of occurrence of *S. jordani* is 7.7% off central California and decreases to 5.7% off southern California and 1.5% off northern Baja California (Table 14). Percentage of *S. jordani* larvae to total *Sebastes* larvae was highest (20%) off southern California. Spawning occurs over a short time period compared with other species studied (Table 15); it extends from January to April with a peak in February or March.

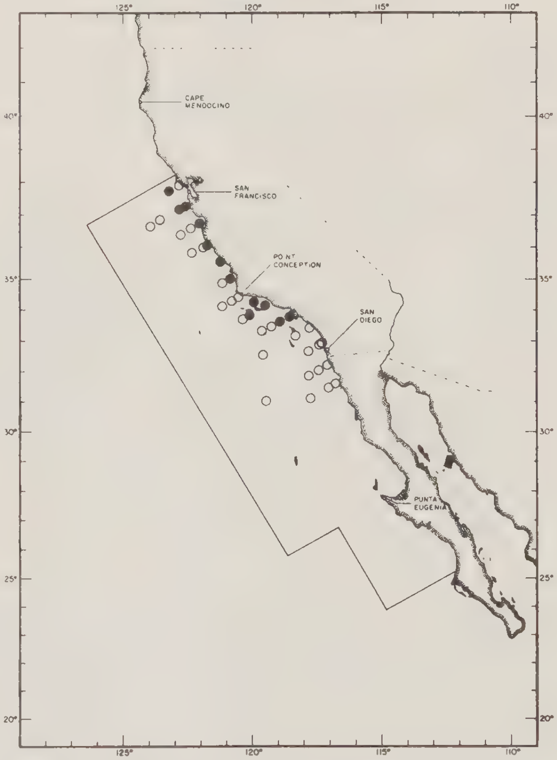

Figure 10.—Stations at which larvae of *Sebastes jordani* were collected by CalCOFI plankton surveys during 1966. Solid circles indicate stations where number of larvae exceeded mean number (43.8) for all positive stations. Area of frequent occupancy is outlined.

Table 14. Relative abundance and frequency of occurrence of Sebastes jordani in CalCOFI collections for 1966.

CalCOFI regions and lines	Total stations occupied	Total stations containing Sebastes larvae	Percentage of stations containing Sebastes	Total stations containing S. jordani	Percentage of stations containing S. jordani	Standardized number of S. jordani larvae	Standardized number of Sebastes larvae in hauls containing S. jordani	Percentage of S. jordani larvae to total Sebastes larvae
Central California 60-77	235	56	23.8	18	7.7	992	8,562	11.6
Southern California 80-93	511	263	51.5	29	5.7	1,355	6,822	19.9
Northern Baja California 97-107	459	122	26.6	7	1.5	40	692	5.8
Upper central Baja California 110-120	418	91	21.8	0	0	0	0	0
Lower central Baja California 123-137	325	36	11.1	0	0	0	0	0

Table 15. Standardized numbers (A), mean length in mm with standard deviation (B), and size range in mm of Sebastes jordani larvae taken on CalCOFI cruises of 1966. There was no cruise during March, and S. jordani were not taken from May to December. Stations in central California were not occupied in February.

CalCOFI regions and lines	January			February			April		
	A	B	C	A	B	C	A	B	C
Central California 60-77	781.9	4.9 ± 0.59	4.0 - 7.0	-	-	-	205.2	7.5 ± 3.31	5.1 - 24.5
Southern California 80-93	459.0	5.1 ± 1.01	4.5 - 8.0	863.3	4.9 +1.51	4.4 - 8.0	54.6	5.8 ± 1.38	5.0 - 11.0
Northern Baja California 97-107	0	0	0	15.3	6.8 ±1.49	5.2 - 10.0	0	0	0

Sebastes levis (Eigenmann and Eigenmann), Figure 11

Literature.—Newborn larvae of *S. levis*, the cow rockfish or cowcod, were illustrated in Moser (1967a).

Distinguishing features.—Larvae of *S. levis* are about 5.0 mm long at birth; they achieve the relatively large size of about 20 mm. A specimen 21.3 mm was just beginning to develop the lateral pigment saddles typical of pelagic juveniles, whereas transformation has progressed far enough in a 19.1-mm specimen to classify it as a pelagic juvenile. The pelagic juvenile phase appears to be protracted since pelagic juveniles up to 58 mm were taken in midwater trawls and the smallest demersal juvenile found was 66.5 mm.

The large fanlike pectoral fins are diagnostic features of cow rockfish larvae and attain the greatest size of any species of *Sebastes* in the CalCOFI collections. Their length increases from 9% of the body length in newborn larvae to 46% at the completion of notochord flexion (Table 16). Pectoral fin length in the few large larval specimens is 41 to 45% of the body length. The large pectoral fins are characteristic of pelagic juveniles; 19- and 33-mm specimens had fin lengths 46 and 47% of the body length. In larger pelagic juveniles the pectorals become relatively smaller; fin length in a 47-mm specimen was 38% of the body length and in a 58-mm specimen it was 32%.

The melanistic pigmentation of cow rockfish larvae is also an aid to identification. Newborn larvae have a melanistic shield over the gut, a patch of melanophores over the brain, heavy pigmentation on the tip of the lower jaw, and a moderate number of melanophores in the ventral midline series (mean of 17 with a range of 13 to 22 for 20 specimens counted). The pectoral fin is covered with fine melanophores that are concentrated in a band at the distal margin. With the rapid growth of the fin in larvae between 6 and 7 mm, the melanophores on the major part of the pectoral are lost but the marginal band remains prominent. With further development, the marginal band widens so that in larvae of 11 mm the fin is covered solidly with fine melanophores. This pigment is retained in pelagic juveniles. When the larvae transform into pelagic juveniles at about 20 mm, pigment saddles begin to develop along the anterior region of the trunk. Additional saddles develop posteriorly and with further enlargement they become distinct bands. These are evident in pelagic juveniles as small as 33 mm and are retained in demersal juveniles and adults.

Table 16. Measurements (mm) of Sebastes levis larvae. (Specimens between dashed lines are undergoing notochord flexion.)

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-anal fin distance
5.0	2.0	2	0.26	0.38	0.90	0.43	0.40		-
7.6	3.4	2.2	0.75	0.66	1.8	1.8	0.90	0.12	-
8.7	4.1	2.4	0.82	0.77	2.4	2.8	1.2	0.34	5.0
8.9	4.2	2.9	1.0	0.91	2.5	3.2	1.2	0.51	5.2
9.2	4.3	2.8	1.0	0.92	2.3	2.9	1.2	0.44	5.4
9.4	4.7	2.9	1.0	0.93	2.8	3.5	1.2	0.50	5.2
9.8	4.7	2.8	1.0	0.90	2.6	2.9	1.2	0.50	5.8
10.1	5.2	3.1	1.1	1.1	3.1	4.2	1.3	1.0	5.8
10.4	5.8	3.4	1.2	1.2	3.6	4.8	1.3	1.2	6.2
11.3	6.4	4.3	1.2	1.2	3.7	5.0	1.3	1.8	6.8
12.3	7.0	4.2	1.3	1.3	4.2	5.1	1.5	2.2	7.4
21.3	13.5	7.2	2.1	2.2	7.1	9.6	2.4	5.1	13.8
*19.1	11.8	6.3	1.8	2.0	7.1	8.7	2.1	4.8	12.2
*32.8	20.9	10.8	3.0	2.8	11.2	15.4	3.5	9.2	21.9
*47.5	29.9	16.4	5.2	4.1	16.2	18.2	4.8	10.6	31.0
*58.4	36.8	20.1	6.7	5.0	20.3	18.9	5.4	13.0	38.5
**66.5	42.3	24.1	6.7	6.0	22.4	19.5	6.6	14.7	43.1

*Pelagic juvenile.

**Benthic juvenile.

Distribution.—Adult cow rockfish have a comparatively limited geographic range from central California to central Baja California with a principal distribution off southern California. The larvae are rare in CalCOFI samples; only 30 (standardized number) were found in collections from 1951, 1952, 1953, 1961, and 1969. Their geographic distribution suggests that, in terms of reproduction, the cow rockfish is essentially a species of the California Bight (Fig. 12). Cow rockfish larvae were taken from January to June but in such low numbers that months of maximum abundance could not be determined.

Sebastes cortezi (Beebe and Tee-Van), Figure 13

Literature.—The literature contains no descriptions of *Sebastes* larvae from the Gulf of California. The taxonomy of adult *Sebastes* in the Gulf is poorly known; however, Chen (1975) has recently reviewed the species of *Sebastes* from these waters. The larval series described herein as *S. cortezi* was identified by meristic characters and transitional specimens provided by Chen.

Distinguishing features.—At birth, *S. cortezi* larvae, like *Sebastes* larvae of the outer coast are 4.0 to 5.0 mm long. The largest specimen in the series (17.1 mm) was beginning to transform.

The most notable morphological features of *S. cortezi* larvae are the short pectoral fins which have a slight dorsad orientation for most of the larval period, and the

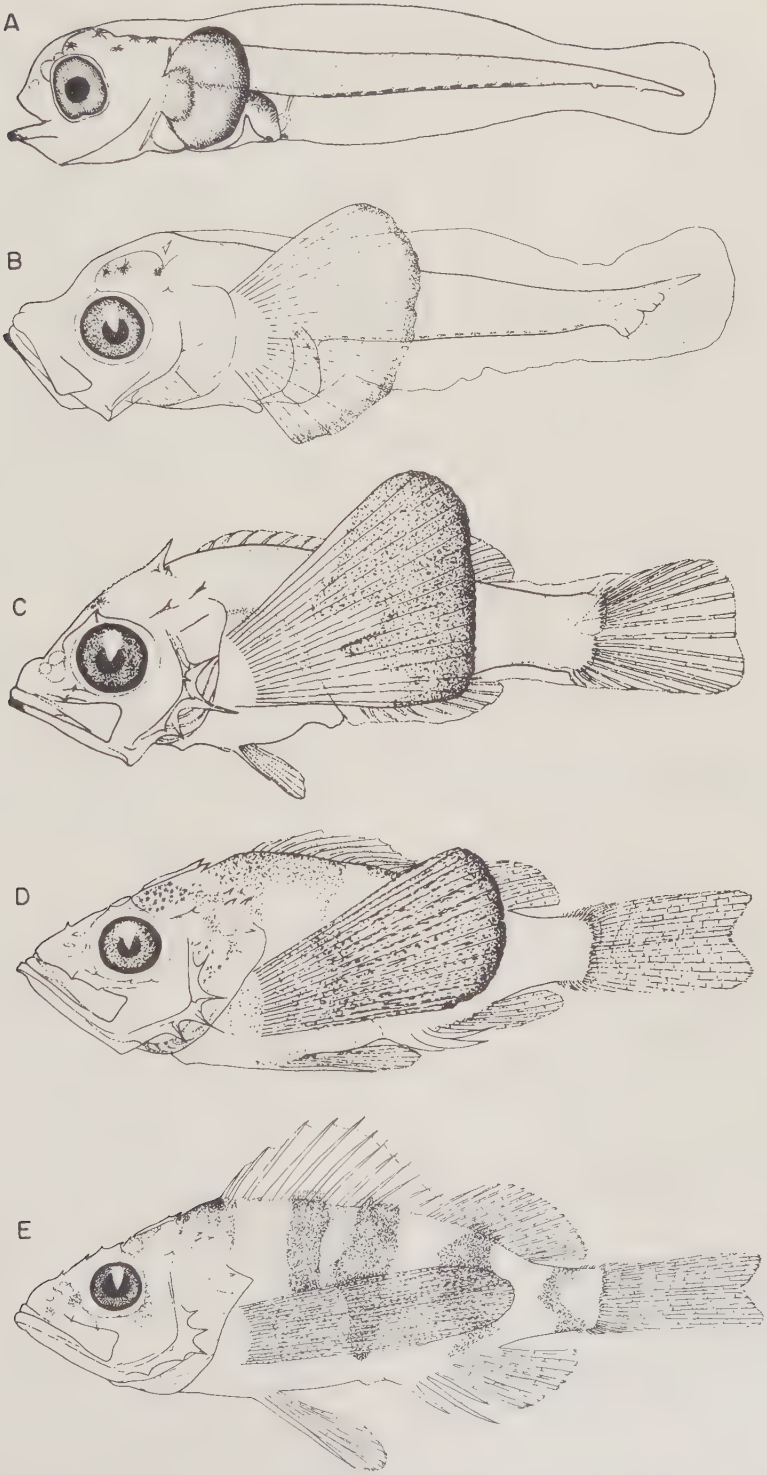

Figure 11.—Developmental series of *Sebastes levis*. A. 5.0-mm larva; B. 7.2-mm larva; C. 10.4-mm larva; D. 19.1-mm transforming specimen; E. 32.8-mm pelagic juvenile.

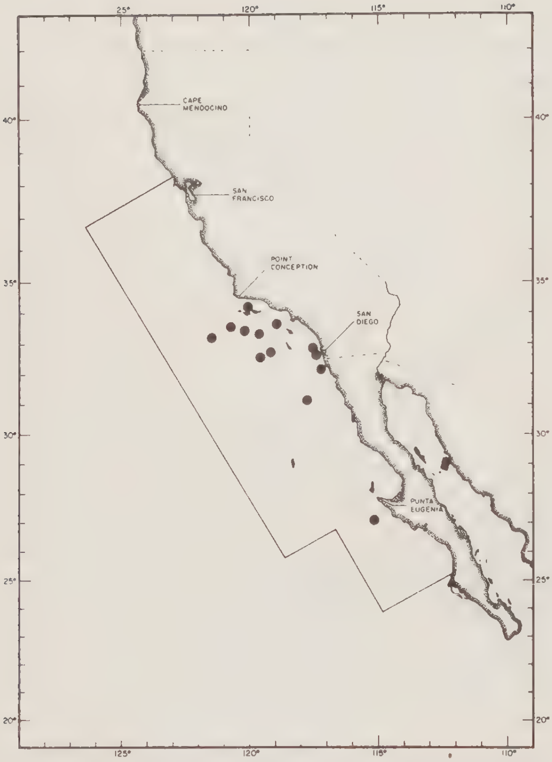

Figure 12.—Stations at which larvae of *Sebastes levis* were taken during 4 yr (1951, 1955, 1968, and 1969) of CalCOFI plankton surveys. Area of total grid is outlined.

length of parietal spines. Pectoral fin length is 7 to 9% of the body length in larvae up to the beginning of notochord flexion, 9 to 12% during notochord flexion, and has increased to a maximum of 21% following notochord flexion. It is 23% in the transforming specimen (Table 17). A morphological feature which helps to distinguish *S. cortezi* larvae from Type A Gulf larvae is the length of the parietal spines, the spines being relatively shorter in *S. cortezi*. In larvae between 8.0 and 9.0 mm, when the spines reach their greatest length relative to the head length, those of *S. cortezi* are 21 to 22% of the head length and those of Type A are 25 to 34%.

Table 17. Measurements (mm) of larvae of Sebastes cortezi. (Specimens between dashed lines are undergoing notochord flexion.)

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-anal fin distance
4.1	1.7	1.0	0.25	0.34	0.75	0.37	0.28	---	...
4.5	1.8	1.2	0.30	0.38	0.95	0.30	0.40	---	...
4.7	1.9	1.2	0.37	0.47	1.2	0.37	0.38	---	...
5.1	2.2	1.5	0.43	0.49	1.3	---	---	---	...
5.7	2.5	1.7	0.48	0.54	1.3	0.41	0.57	---	...
6.1	2.6	1.7	0.52	0.55	1.4	0.57	0.60	---	...
6.4	2.9	1.9	0.63	0.60	1.6	0.60	0.64	0.06	---
7.0	3.5	2.1	0.68	0.78	---	0.65	0.82	0.07	4.2
7.2	3.7	2.2	0.78	0.85	2.0	0.73	0.90	0.10	4.2
7.8	3.8	2.5	0.75	0.86	2.1	0.77	0.91	0.14	4.5
8.0	4.0	2.7	0.75	0.94	2.2	0.93	0.94	0.15	4.7
8.3	4.8	2.6	---	0.90	2.3	1.0	0.92	0.15	4.9
8.8	4.5	2.6	0.90	1.0	2.5	1.0	1.0	0.16	5.2
11.8	7.5	4.4	1.4	1.4	4.1	2.3	1.4	1.5	7.8
12.5	7.8	4.7	1.5	1.4	4.2	2.6	1.2	1.5	8.1
13.5	8.9	5.5	---	1.4	4.3	2.6	1.3	1.6	9.3
*17.1	10.3	6.3	1.9	1.8	5.6	3.9	1.6	2.5	10.8

*Transforming specimen.

Melanistic pigmentation is more useful than morphology in distinguishing *S. cortezi* larvae from other rockfish larvae. At birth the larvae have the usual pigment shield over the gut and a series of melanophores along the ventral midline of the tail (mean of 15 with a range of 10 to 21 melanophores for 15 larvae counted). A large melanophore is located in the position of the future caudal fin and remains there throughout the larval period. The pectoral fins have an unusual pigment pattern; there is a melanistic patch in the proximal ventral sector of the fin and the dorsal and distal portions are clear. With further development, the entire proximal region becomes pigmented but the distal clear zone widens. The medial surface of the fin base is covered with large melanophores. The pelvic fins are pigmented in larvae 11.8 mm and larger.

Other pigment develops above the brain and, late in the larval period, on other regions of the head. In larvae about 8.0 mm long a short series of five to six pairs of melanophores develops along the dorsal midline of the tail. With further development this series lengthens, and extends along the entire dorsum in larvae 12.5 mm and longer. The ventral series of melanophores becomes restricted to the caudal peduncle after the anal fin is developed (about 8.0 mm). The 11.8-mm larva has a large patch of melanophores on the lateral surface of the caudal peduncle. In later stages, melanophores extend anteriad along the lateral line from this patch and, in the 17.1-mm specimen, the entire trunk above the lateral line is becoming pigmented.

Distribution.—Eight CalCOFI cruises into the Gulf of California in 1956 and 1957 and a U.N. Food and Agriculture Organization (FAO) cruise in March of 1972 provide information on the distribution and abundance of *S. cortezi* larvae. Like the adults (Chen 1975), the larvae occur in the western side of the Gulf and range latitudinally from off Point San Fermin south to about Carmen Island (Fig. 14). Most of the larvae were taken just north and just south of the large islands, Tiburon and Angel de la Guarda, in the upper Gulf. Although the results of the various cruises are not strictly comparable because they differed in area covered and in the number of stations occupied, Table 18 gives some indication of the seasonality of spawning. Larvae are present during the cold-water months and appear to have a maximum abundance in March.

Table 18. Mean length (mm) with total standardized number of larvae of Sebastes cortezi and S. Type A in plankton collections from the Gulf of California.

Species	February		March		April		June
	$\bar{x}$ length	Standard number	$\bar{x}$ length	Standard number	$\bar{x}$ length	Standard number	Standard number
S. cortezi	4.3	31	7.2	121	6.2	23	0
S. Type A	5.2	177	6.5	75	6.6	25	0

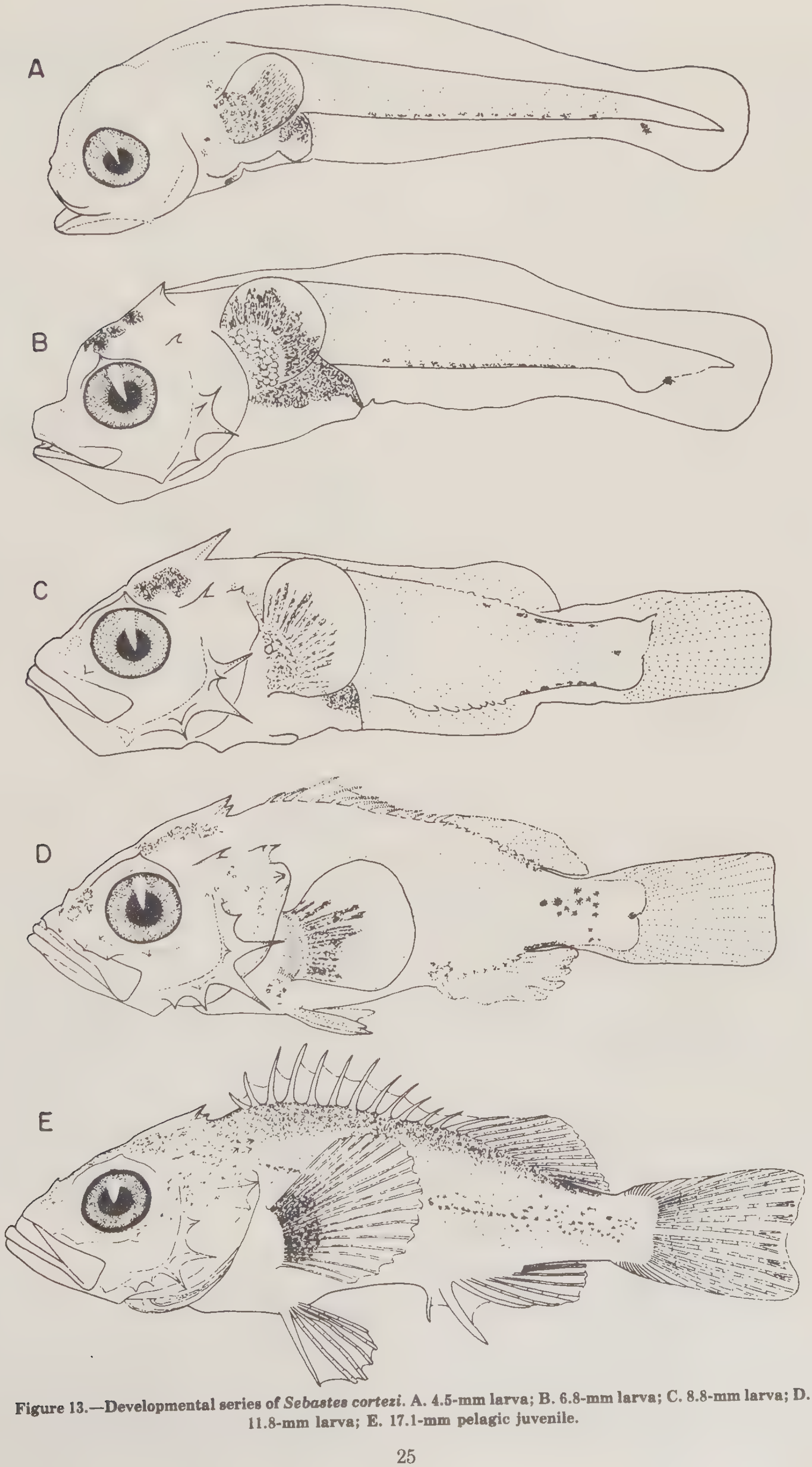

Figure 13.—Developmental series of *Sebastes cortezi*. A. 4.5-mm larva; B. 6.8-mm larva; C. 8.8-mm larva; D. 11.8-mm larva; E. 17.1-mm pelagic juvenile.

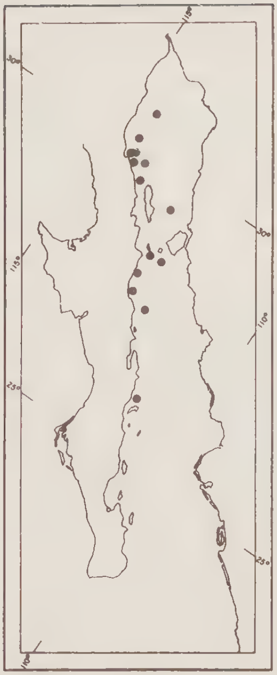

Figure 14.—Stations in the Gulf of California at which larvae of *Sebastes cortezi* were taken on CalCOFI cruises during 1956 and 1957.

***Sebastes* sp.—Gulf of California Type A, Figure 15**

Literature.—See previous species account.

Distinguishing features.—At birth, Type A larvae are 4.0 to 5.0 mm long. The maximum size obtained before transformation is not known since the largest larva in the collection is 10.8 mm.

Type A larvae, like those of *S. cortezi*, have short pectoral fins. Pectoral fin length is 6 to 9% of the body length before onset of notochord flexion, and thereafter increases to 20% in the longest larva (Table 19). At comparable sizes, the parietal spines are longer in Type A than in *S. cortezi*.

Type A larvae have a distinctive pattern of melanophores. As in *S. cortezi*, newborn larvae of Type A have a shield of pigment over the gut and a series of melanophores along the ventral midline of the tail (mean of 16 with a range of 12 to 21 for 13 larvae). Unlike *S. cortezi* larvae, those of Type A have a blotch of pigment at the symphysis of the lower jaw, that persists in larvae up to about 8 mm. The pectoral fins have fine melanophores distributed over the entire blade of the fin and have the medial surface of the fin base covered with large melanophores. At about 8 mm, pigment appears above the brain. No pigment forms on the dorsal surface of the tail as in *S. cortezi*. The pigment pattern is similar to that of the subgenus *Sebastomus* from outer coastal waters, suggesting that Type A larvae might be referable to *S.* (*Sebastomus*) *exsul.*

Table 19. Measurements (mm) of larvae of Sebastes sp. [Gulf of California Type A]. (Specimens between dashed lines are undergoing notochord flexion.)

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-anal fin distance
4.2	1.5	0.84	0.23	0.33	0.78	0.33	0.22	---	---
4.7	1.8	1.00	0.28	0.35	0.80	0.30	0.32	---	---
5.4	2.2	1.3	0.37	0.45	1.1	0.47	0.43	---	---
5.8	2.4	1.5	0.41	0.48	1.2	0.54	0.55	---	---
6.1	2.6	1.7	0.48	0.50	1.4	0.61	0.58	---	---
6.4	2.6	1.7	0.50	0.55	1.4	0.63	0.60	---	---
7.0	3.6	2.4	0.90	0.73	2.1	0.90	0.90	---	4.3
7.3	3.4	2.3	0.82	0.69	1.9	0.81	0.82	0.09	4.3
7.6	4.2	2.7	0.92	0.86	2.4	1.2	1.0	0.25	4.7
8.2	4.3	2.7	1.0	0.90	2.7	1.2	1.1	0.44	4.8
8.5	4.4	2.9	1.0	0.95	2.5	1.2	1.2	0.32	5.2
9.5	5.4	3.5	1.2	1.1	3.2	1.7	1.2	0.80	5.7
10.8	6.8	4.4	1.4	1.4	3.8	2.2	1.2	0.70	7.2

Distribution.—Eight CalCOFI cruises into the Gulf in 1956 and 1957 and an FAO cruise in March of 1972, provide information on the distribution and abundance of Type A larvae. Their latitudinal range, from Gonzaga Bay south to Concepcion Bay, is more constricted than that of *S. cortezi*, but they are not nearly so restricted to the western side of the Gulf as are larvae of *S. cortezi* (Fig. 16). Their heaviest concentration is around Tiburon and Angel de la Guarda islands in the upper Gulf. Table 18 shows that spawning occurs during the cold-water months with a possible peak in February.

***Sebastes marinus* (Linnaeus), Figure 17**

Literature.—The numerous descriptions and illustrations of intraovarian and planktonic larvae of North Atlantic *Sebastes* were cited above in the literature review for the genus. Those of Tåning (1961) are especially useful, since they incorporate observations on chromatophores that can only be made in live material. A series of illustrations from Tåning's (1961) paper are reproduced here. The larvae used for our study are from the *Dana* collections and were identified by A. V. Tåning, but Eschmeyer (pers. commun.) has suggested that the series may contain some specimens of *S. mentella* and that the identification should be considered tentative until additional material is available. These were measured to establish a table of morphometrics, which to our knowledge has not yet appeared in the literature. The following description, which includes morphometric and other previously overlooked characters, is intended as a supplement to the extensive literature on *S. marinus* larvae.

Distinguishing features.—At birth the larvae of *S. marinus* are considerably larger than those of the eastern Pacific species. A series of full-term intraovarian larvae ranged in length from 6.7 to 7.2 mm. Also, they reach a comparatively large size before undergoing a gradual transformation into pelagic juveniles. In the measured series the transition occurs at about 24 mm (Table 20).

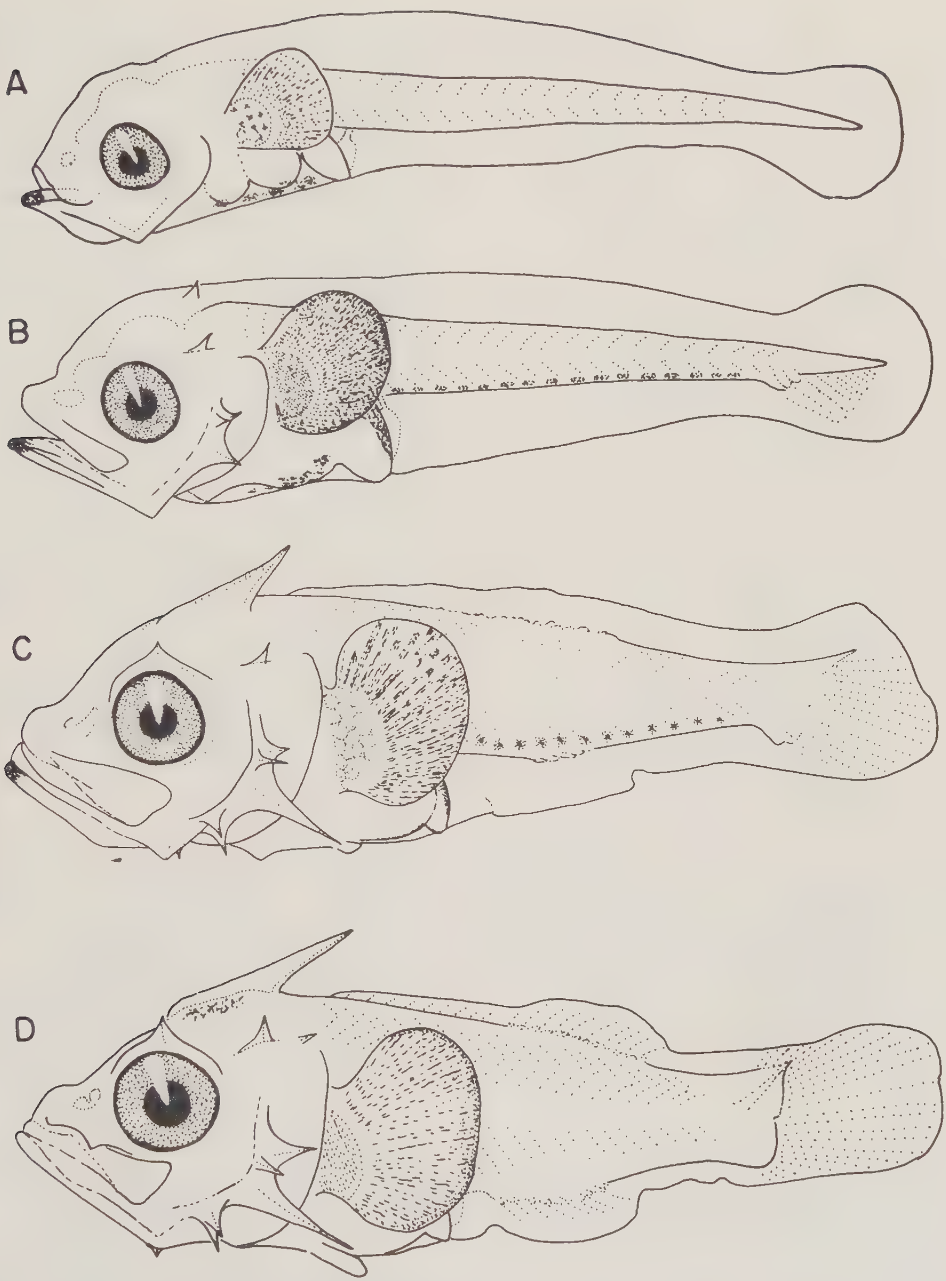

Figure 15.—Larvae of *Sebastes* Gulf of California Type A. A. 4.7 mm; B. 6.2 mm; C. 7.2 mm; D. 8.3 mm.

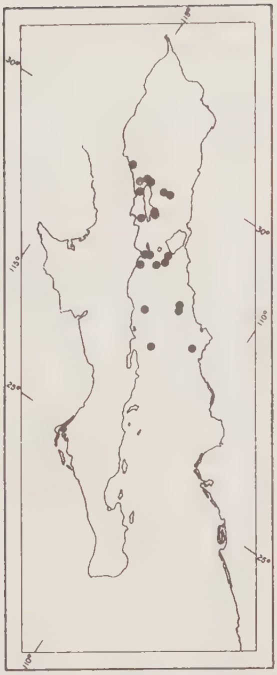

Figure 16.—Stations in the Gulf of California at which larvae of *Sebastes* Gulf of California Type A were taken on CalCOFI cruises during 1956 and 1957.

Table 20. Measurements (mm) of larvae of Sebastes marinus. (Specimens between dashed lines are undergoing notochord flexion.)

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-anal fin distance
7.1	2.2	1.2	0.33	0.51	1.3	0.18	0.26	---	-
7.3	2.9	1.8	0.50	0.66	1.4	0.50	0.55	-	
8.1	2.9	1.8	0.48	0.73	1.4	0.58	0.61	---	---
8.5	3.2	2.1	0.55	0.78	1.6	0.68	0.66	0.04	4.5
9.0	3.8	2.5	0.73	0.87	1.9	0.75	0.74	0.06	4.1
9.3	3.9	2.5	0.68	0.86	1.8	0.74	0.75	0.09	5.3
9.6	4.0	2.7	0.75	0.91	1.9	0.82	0.80	0.12	5.6
10.0	4.5	2.8	0.93	1.0	2.2	1.0	0.82	0.15	5.7
10.6	4.8	3.2	1.0	1.1	2.3	1.1	0.87	0.18	6.0
11.0	5.2	3.3	1.0	1.2	2.3	1.2	1.0	0.20	6.2
11.3	5.8	3.7	1.2	1.2	2.6	1.4	1.0	0.40	6.8
11.8	6.4	4.0	1.2	1.3	3.1	1.5	1.0	0.41	7.4
12.7	7.0	4.2	1.3	1.5	3.2	1.8	1.2	0.60	7.8
13.5	7.3	4.5	1.5	1.5	3.4	2.0	1.2	0.75	8.2
14.4	8.3	4.8	1.5	1.8	4.0	2.2	1.3	1.2	9.0
15.0	8.8	4.9	1.6	1.7	3.9	2.3	1.3	1.2	9.4
16.6	9.8	5.8	2.0	1.9	4.3	2.6	1.3	1.5	10.3
17.2	10.0	5.8	1.7	2.2	4.2	3.2	1.4	1.8	10.5
18.4	10.2	5.8	1.7	2.3	4.6	3.3	1.4	1.9	10.6
19.3	11.0	6.6	2.1	2.4	4.9	3.5	1.6	2.1	11.7
20.5	11.7	6.7	2.0	2.4	4.9	3.8	1.5	2.3	12.3
22.3	12.8	7.1	2.1	2.6	5.2	4.2	1.7	2.8	13.4
*24.1	14.0	7.7	2.1	2.8	5.9	4.8	1.9	2.9	14.9
*26.0	15.4	8.7	2.4	3.0	6.5	5.8	2.1	3.6	16.2
*28.1	16.6	8.7	2.5	3.0	6.8	6.3	2.2	3.8	17.6
*30.4	18.2	9.4	2.9	3.2	7.7	6.8	2.3	4.3	19.3
*38.7	22.9	11.2	3.1	3.8	8.9	9.2	2.8	6.0	24.8

*Pelagic juvenile.

The larvae are more slender than all but the slenderest of eastern Pacific *Sebastes*, such as *S. jordani*, which they resemble in a number of other characters. Body depth averaged 18% of body length in preflexion larvae, 21% during flexion, and 25% in postflexion larvae and early pelagic juveniles.

The gut is compact and relatively shorter than most eastern Pacific *Sebastes*. In larvae less than 10 mm, the relative snout-anus length is equal to or less than in *Sebastes jordani* (Fig. 18). In developmental stages larger than this, relative snout-anus length is intermediate between *S. jordani* and the other eastern Pacific species measured. Snout-anus distance increases from an average of 35% of body length in preflexion larvae to 45% during notochord flexion, and further to 58% in postflexion larvae and small pelagic juveniles.

The head is relatively small as in other species of *Sebastes*. Head length averages 21% of the body length in preflexion larvae, 29% in larvae undergoing flexion, and 32% in postflexion larvae and small pelagic juveniles. Snout length averages 28% of head length in preflexion larvae, increases to an average of 31% in later larval stages, and then decreases slightly to an average of 29% in small pelagic juveniles. Relative eye diameter is greatest in preflexion larvae (mean of 40% of head length) and then decreases to a mean of 35% of head length in later developmental stages.

A prominent feature of *S. marinus* larvae is their relatively short rounded pectoral fins. Fin length averages 6% of body length before notochord flexion, 10% during flexion, 17% in postflexion larvae, and 22% in small juveniles. Relative fin length is less than in all eastern Pacific species studied with the exception of *S. jordani* which has similarly small pectorals (Fig. 19). Pelagic juveniles of *S. marinus* have a slightly longer pectoral fin than in pelagic juveniles of *S. jordani* (Fig. 19). The sequence of ossification of the pectorals and other fins could not be determined because of calcium leaching in the Formalin-preserved specimens.

The pigment pattern of *S. marinus* larvae is similar to that of other North Atlantic *Sebastes* species and is also similar to that of *S. jordani* of the eastern Pacific. Newborn larvae have a group of melanophores above the optic lobes of the brain, a melanistic shield over the dorsolateral surface of the gut, an embedded spot at the nape, and a series of melanophores along the ventral and dorsal midlines of the tail. The ventral row begins at the 4th to 7th postanal myomere and extends to the 19th to 22nd postanal myomere. In a sample of 18 full-term intraovarian larvae, the total number of melanophores in the ventral row ranged from 11 to 24 with a mean of 18.0 ± 4.07 SD. The dorsal row is shorter, beginning on the 10th to 15th postanal myomere and ending on the 18th to 22nd postanal myomere; the number of melanophores ranged from 8 to 21, with a mean of 13.1 ± 3.16 for the 18 specimens.

The ventral midline series of *S. marinus* is shorter and contains fewer melanophores than in larvae of the other North Atlantic species and in *S. jordani* of the Pacific. In 120 newborn specimens of the American form, the number of ventral melanophores ranged from 26 to 42 and in three newborn specimens of *S. viviparus* from the Faeroe Islands the number ranged from 18 to 29. In 15 specimens

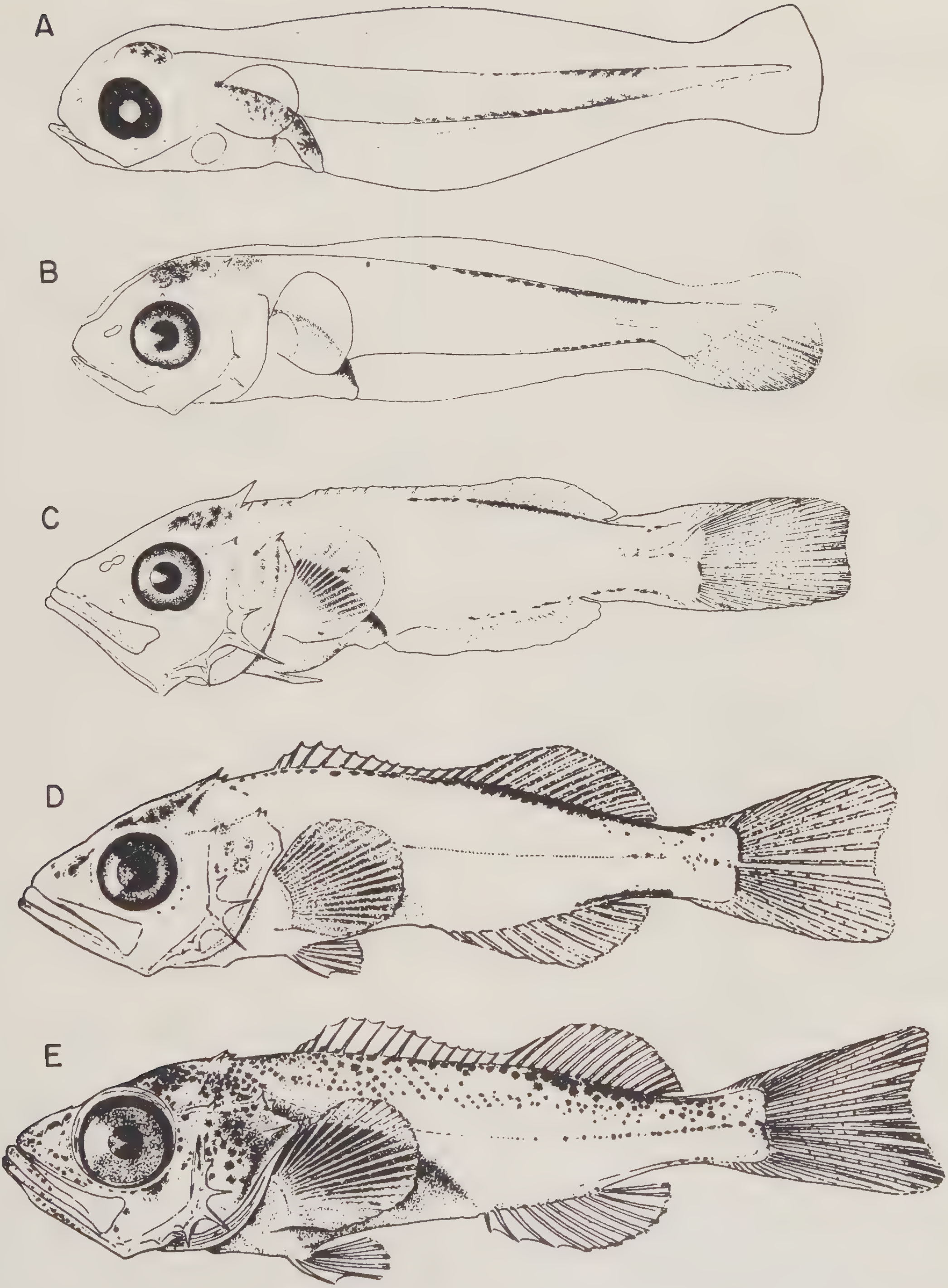

Figure 17.—Developmental series of *Sebastes marinus* from Táning (1961). A. 6.8-mm larva; B. 10.5-mm larva; C. 15.7-mm larva; D. 20.9-mm larva; E. 27.0-mm pelagic juvenile.

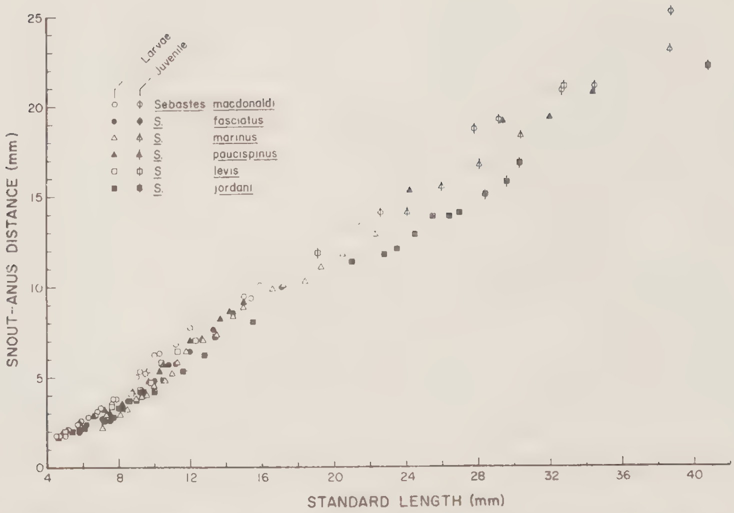

Figure 18.—Relation of snout-anus length to body length in developmental stages of *Sebastes* spp.

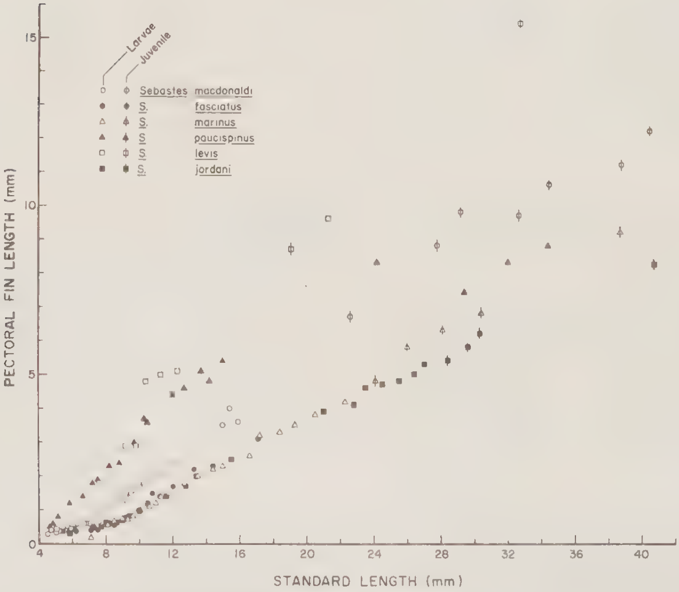

Figure 19.—Relation of pectoral fin length to body length in developmental stages of *Sebastes* spp.

of *S. jordani*, the number of ventral melanophores ranged from 21 to 27 with a mean of 23.7 ± 1.75 SD. Larvae of *S. marinus* differ also from those of the American form and *S. viviparus* in lacking the one to several caudal melanophores present in these latter species.

The dorsal and ventral midline pigment series of *S. marinus* larvae have opposite fates. The ventral series becomes embedded in the developing musculature and obscured by the developing anal fin. At the completion of notochord flexion only those melanophores posterior to the anal fin are visible. The dorsal series is augmented anteriad and in 9-mm larvae divides into two streaks, one on each side of the developing dorsal fin. When the larvae reach 14.5 mm the streaks extend anteriad along the entire dorsum.

In addition to the initial pigment pattern, melanophores are added gradually to the head region. In 9-mm larvae a pair of melanophores appears on the ventrolateral surface of the medulla, the olfactory region of the brain becomes covered with a patch of melanophores, and a pair of melanistic streaks appears along the premaxillaries. At about 11.0 mm, a melanistic patch appears on the opercle and enlarges with further development. At about 12.5 mm, a blotch appears at the symphysis of the lower jaw. In 15-mm larvae, blotches appear around the nares, ventroposterior to the eyes, and at the isthmus. At about 17.0 mm, melanophores cover most of the dorsal and lateral surfaces of the head.

On the body the initial pigment pattern is augmented by the appearance of melanophores at the posterior edge of the hypural plates in 9-mm larvae. At the completion of notochord flexion, the posterior edge of each hypural plate is outlined by a pigment streak. At about 10.0 mm, deeply embedded pigment begins to form along the dorsal aspect of the more posterior vertebral centra. This spreads anteriorly and at about 16.0 mm the dorsal aspect of the entire vertebral column is covered. At about 13.5 mm a line of melanophores forms along the posterior segment of the lateral line and extends progressively anteriad with further larval development. Also, each of the distal radial elements of the dorsal fin develops a melanistic spot as do the distal radials of the anal fin in 15-mm larvae.

The epaxial region of the trunk begins to be covered with melanophores in 16-mm larvae. These are concentrated along the myosepta. At about 24.0 mm the entire half of the trunk above the lateral line is covered, marking the transition to the pelagic juvenile phase. The pectoral and pelvic fins develop no melanistic pigmentation in larvae or pelagic juveniles.

Distribution.—The geographic and bathymetric distribution of *Sebastes* in the North Atlantic is the subject of an enormous literature and need not be discussed here. Much of the information on distribution of adults is summarized in Templeman (1959) and in the proceedings of an international symposium on redfish (Templeman 1961), although most of his references to *S. marinus mentella* refer to *S. fasciatus* (Eschmeyer, pers. commun.). The symposium proceedings also contain a summary of information on distribution of larvae (Einarsson 1961).

Sebastes viviparus (Krøyer), Figure 20

Literature.—Literature references on *S. viviparus* larvae were cited in the literature review for the genus. In the earlier literature, larvae of *S. viviparus* were sometimes confused with *S. marinus*. Templeman and Sandeman (1959) have reviewed this literature and attempted to correct the errors. The two most useful papers on *S. viviparus* larvae are by Tåning (1961) and Einarsson (1960). In these papers, larvae of *S. viviparus* and *S. marinus* are described and compared with emphasis on the differentiating characters of pigmentation and spination.

A series of larvae up to 10.6 mm was obtained from the collections of the *Dana* Expeditions and measured to provide a table of morphometrics for comparison with other North Atlantic species (Table 21). This is presented with a brief description that incorporates previously unreported characters together with those of Tåning (1961)

Table 21. Measurements (mm) of larvae of Sebastes viviparus. (Specimens between dashed lines are undergoing notochord flexion.)

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-anal fin distance
5.4	2.0	1.2	0.28	0.55	1.0	0.35	0.43	---	---
5.9	2.2	1.2	0.37	0.57	1.2	0.53	0.44	---	---
6.5	2.4	1.3	0.32	0.59	1.2	0.40	0.41	---	---
6.8	2.3	1.3	0.31	0.60	1.2	0.45	0.46	---	---
7.0	2.8	1.8	0.48	0.72	1.5	0.57	0.56	---	---
7.3	2.9	1.9	0.50	0.74	1.5	0.55	0.63	---	---
7.8	3.0	1.9	0.50	0.80	1.7	0.62	0.69	---	---
8.0	3.2	2.0	0.58	0.82	1.7	0.62	0.68	---	3.7
8.5	3.7	2.3	0.69	0.92	1.8	0.78	0.80	0.13	4.6
9.0	3.9	2.6	0.78	1.0	2.1	0.90	0.95	0.19	5.1
9.4	4.2	2.8	0.86	1.0	2.2	0.92	1.0	0.17	5.3
9.9	4.5	2.9	0.97	1.1	2.3	1.1	1.0	0.18	5.7
10.4	4.8	3.2	1.0	1.2	2.4	1.2	1.0	0.28	6.1
10.6	5.2	3.3	1.0	1.2	2.6	1.2	0.90	0.23	6.2

Distinguishing features.—*Sebastes viviparus* larvae are born at a size 1 to 2 mm smaller than *S. marinus* larvae. Tåning (1961) illustrated a 5.8-mm full-term intraovarian larva of *S. viviparus*; the smallest planktonic larvae in our series was 5.4 mm. Other developmental events also occur at a smaller size in *S. viviparus* compared with *S. marinus*. Notochord flexion begins at about 7.8 mm in our series and is completed at about 10.6 mm. In *S. marinus* it begins at about 8.5 mm and is completed at about 11.8 mm. Einarsson (1960) and Tåning (1961) pointed out that development of the head spines, particularly the preopercular series, is at a relatively advanced state in *S. viviparus* larvae of the same size as those of *S. marinus*. The size at transformation into the pelagic juvenile stage cannot be ascertained from our series since the largest larva is 10.6 mm. There are no literature references to size at transformation for this species.

Developmental changes in body proportions follow those of *S. marinus* with some apparent differences in mean values for the principal larval stages. Means for relative eye diameter, body depth, and pectoral fin base depth are greater than in *S. marinus* for preflexion larvae and larvae undergoing notochord flexion (Table 22).

The pattern of melanistic pigmentation is similar to that of *S. marinus*; however, the presence of one or more caudal melanophores in *S. viviparus* larvae separates this species from *S. marinus* (Templeman and Sandeman 1959; Einarsson 1960; Tåning 1961). The incompleteness of our series precludes a thorough comparison of pigment pattern in *S. viviparus* with those of other North Atlantic species, but, we have discovered some previously unreported differences.

Pigment features develop in smaller sized larvae of *S. viviparus* compared with *S. marinus*. Several heretofore unreported features begin to appear in larvae about 6.0 mm long. A group of melanophores form at the tip of the snout and remain prominent up to the termination of our series at 10.6 mm. Although a melanophore may be present in this region in occasional specimens of *S. marinus*

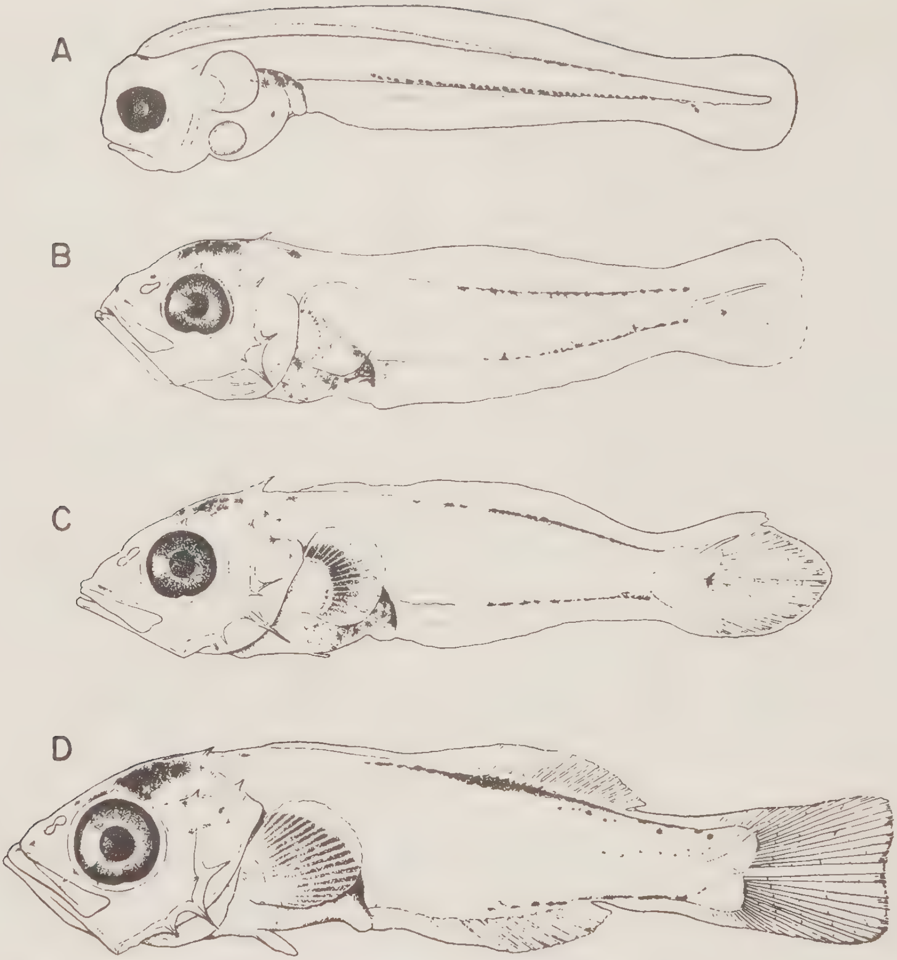

Figure 20.—Larvae of *Sebastes viviparus* from Táning (1961). A. 5.8 mm; B. 8.9 mm; C. 10.1 mm; D. 13.5 mm.

TABLE 22. Morphometric comparison of larvae of three species of Sebastes from the North Atlantic. Mean percentage and range of body proportions are given for preflexion (A), flexion (B), and postflexion (C) larvae. Measurements in mm.

Sebastes		Snout-anus distance / SL		Head length / SL		Snout length / Head length		Eye diameter / Head length		Body depth / SL		Pectoral fin length / SL		Pectoral fin base depth / SL		Pelvic fin length / SL		Snout-anal fin distance / SL	
		x̄ ± SD	Range	x̄ ± SD	Range	x̄ ± SD	Range	x̄ ± SD	Range	x̄ ± SD	Range	x̄ ± SD	Range	x̄ ± SD	Range	x̄ ± SD	Range	x̄ + SD	Range
	A	37.2±2.6	34-40	22.0±2.6	19-26	27.6±2.9	23-31	42.8+3.3	38-46	18.4±3.5	13-22	6.2±0.4	6-7	6.7±1.5	6-9	- -	-	- -	-
fasciatus	B	46.0±2.0	44-48	29.0±2.0	27-31	30.0±2.6	28-33	37.7±3.1	35-41	24.7±1.1	24-26	8.0±2.0	6-10	8.3±0.6	8-9	1.6±0.6	1-2	57.3±3.1	54-60
	C	55.2±3.2	51-59	32.7±1.2	31-34	31.0±2.1	27-33	34.8±1.6	33-37	28.2±1.7	26-31	15.3±2.0	13-18	8.7±0.5	8-9	6.8±3.4	3-12	60.2±3.1	58-61
	A	35.7+4.5	31-40	21.3±4.0	17-25	27.7±0.6	27-28	40.3±3.1	37-43	18.0±1.0	17-19	5.7±2.3	3-7	6.7±2.3	4-8	- -	-	- -	-
marinus	B	45.1±5.0	38-54	29.2±2.9	25-34	30.3±3.1	26-36	34.6±1.6	32-37	21.4±2.2	19-26	9.9±1.8	8-13	8.2±0.4	8-9	1.7±1.1	0.5-4	56.3±4.7	53-63
	C	56.9±1.7	54-59	33.2±0.9	32-35	31.2±1.7	29-34	36.2±2.2	33-40	25.1±1.4	23-28	16.8±2.0	14-19	8.3±0.7	7-9	9.1±2.4	5-13	61.0±1.5	58-63
	A	37.5±2.6	34-40	22.2±3.1	19-26	26.0±2.8	24-31	44.0±3.6	39-48	19.5±1.4	18-21	7.3±1.2	6-9	7.5±1.0	6-9	- -	-	- -	-
viviparus	B	43.7±3.4	38-49	28.2±2.7	24-31	30.0±2.0	26-33	38.6±2.2	36-42	22.6±1.3	21-25	9.9±1.5	8-12	9.6±1.1	8-11	2.2±0.4	2-3	55.4±4.5	46-59
	C	- -	-	- -	-	- -	-	- -	-	- -	-	- -	-	- -	-	- -	-	- -	-

and the American form, larvae of these species lack the obvious patch of melanophores that is present in *S. viviparus*. Gut pigmentation is slightly different in *S. viviparus* larvae compared with the other species. The dorsolateral surfaces of the gut are covered with a melanistic shield as in the other species; however, in *S. viviparus* a covering of less densely distributed melanophores extends ventrad over the ventral surface of the gut. The ventral surface of the gut is unpigmented at comparative larval stages in *S. marinus* and *S. fasciatus*.

The most outstanding difference in pigmentation is in the pectoral fins. *Sebastes marinus* and *S. fasciatus* lack pectoral fin pigment throughout the larval period while *S. viviparus* larvae have distinctive pectoral fin pigment. At about 6.0 mm, the medial surface of each fin base begins to develop a covering of melanophores, which remains throughout the larval stages available to us. Also, a series of fine melanophores forms along the bases of the rays and may extend distally for a short distance between the rays in some specimens. This character should be of considerable help in separating larvae of *S. viviparus* from those of other North Atlantic species.

The few early larvae of *S. viviparus* available to us precludes analysis of the number of melanophores in the ventral midline series. Of the three smaller larvae counted, the ventral row began on the 3rd or 4th postanal myomere and terminated on the 19th or 21st myomere. The number of melanophores ranged from 18 to 29 with a mean of 25. This suggests that the mean number of melanophores is greater in *S. viviparus* than in *S. marinus*, a supposition that can only be verified by analysis of an adequate sample of intraovarian larvae.

Distribution.—See Templeman (1961).

Sebastes fasciatus **(Storer), Figure 21**

Literature.—Bigelow and Welsh (1925) briefly described and illustrated a series of *Sebastes* larvae from the Gulf of Maine. Barsukov (1968, 1972) and Barsukov and Zakharov (1972) have established that the common form of this region is specifically distinct and should be referred to as *S. fasciatus* Storer. This is confirmed by Eschmeyer's recent work on gas bladder myology (cited in Hallacher 1974). A larval series of *Sebastes* (Table 23) collected off New England from lat. 38°52′N to lat. 44°22′N by the NMFS Laboratory, Narragansett, is described briefly below and compared with those of *S. marinus* and *S. viviparus*.

Distinguishing features.—It would appear that larvae of this form are born at a smaller size than those of *S. marinus* (Tables 17, 20); however, judging from the appearance of our small specimens of *S. fasciatus*, this difference could be a result of shrinkage in preservative. Larvae of both forms begin notochord flexion at about 8.5 mm; however, flexion is completed at 10.0 mm length in *S. fasciatus* and at about 11.8 mm in *S. marinus*. Information on the size of transformation is not available since the largest larva is 17.1 mm.

Developmental changes in body proportions follow closely those of *S. marinus* and need not be repeated here (Tables 20, 23). One feature which appears to differ is relative body depth. Table 22 shows that mean relative body depth is greater during the three larval phases in *S. fasciatus* than in *S. marinus*. Mean relative eye diameter is greater in *S. fasciatus* than in *S. marinus* for preflexion larvae and larvae undergoing flexion, but is less in postflexion larvae. Mean relative pectoral fin length is greater in *S. fasciatus* than in *S. marinus* in preflexion larvae but is less during and after flexion.

Pigmentation is similar to that of *S. marinus*; however, analysis of our specimens has revealed some differences which have not been previously reported. As in *S. marinus* larvae, the initial pigment pattern consists of a group of melanophores above the brain, a gut shield, an embedded spot at the nape, and a series of melanophores along the dorsal and ventral midlines. There appears to be a difference in the number of melanophores composing the ventral midline series of *S. marinus* and *S. fasciatus* larvae. Ventral melanophores were counted in 10 late-stage intraovarian larvae from each of 12 females of *S. fasciatus* taken in the Gulf of Maine. The mean numbers of melanophores for the 12 samples were as follows: 31.4, 32.2, 32.6, 32.8, 32.8, 33.3, 34.9, 35.2, 35.5, 37.5, 38.3, 40.4. The range for all specimens was 26 to 42. In a sample of 18 *S. marinus* larvae of comparative developmental stage from Greenland, the mean was 18.0 with a range of 11 to 24. Also, the ventral pigment line is relatively longer in *S. fasciatus*, beginning on the 1st to 4th (mean of 2.9 ± 0.40 SD for 112 specimens) postanal myomere and ending on the 19th to 23rd (mean of 21.3 ± 0.85) postanal myomere. In the sample of *S. marinus* the series begins on the 4th to 7th (mean 5.4 ± 0.78 for 18 specimens) postanal myomere and ends on the 19th to 22nd (mean of 20.9 ± 0.86) postanal myomere. The dorsal midline row appears to contain fewer melanophores in *S. fasciatus* compared with *S. marinus*. Mean counts for the 12 samples are: 3.0, 5.4, 6.6, 6.9, 7.2, 7.2, 7.3, 7.6, 7.9, 8.0, 8.6, 9.1. In the sample of *S. marinus* the mean was 13.1 with a range of 8 to 21. In the samples of *S. fasciatus* the dorsal series began on

Table 23. Measurements (mm) of larvae of *Sebastes fasciatus*. (Specimens between dashed lines are undergoing notochord flexion.)

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-anal fin distance
5.8	2.0	1.1	0.25	0.51	1.0	0.35	---	- -	---
6.2	2.4	1.3	0.36	0.58	1.1	0.36	0.40	---	---
7.1	2.7	1.6	0.44	0.71	1.4	0.40	0.42	---	---
7.5	2.6	1.6	0.44	0.66	1.5	0.42	0.43	---	---
8.2	3.3	2.1	0.65	0.80	1.8	0.61	0.72	0.07	4.2
8.5	3.7	2.3	0.77	0.95	2.0	0.55	0.67	0.11	4.6
9.2	4.2	2.7	0.75	1.0	2.2	0.76	0.80	0.15	5.5
10.0	4.8	3.1	0.90	1.1	2.6	1.0	0.85	0.25	5.8
10.8	5.7	3.4	1.1	1.2	3.0	1.5	1.0	0.42	6.3
11.2	5.7	3.6	1.1	1.2	2.9	1.4	1.0	0.37	6.8
12.0	6.4	3.8	1.2	1.4	3.4	1.7	1.1	0.55	7.1
13.3	7.6	4.4	1.2	1.6	3.9	2.2	1.2	1.1	8.1
14.4	8.5	4.9	1.6	1.7	3.9	2.3	1.2	1.3	8.8
17.1	9.9	5.8	1.8	1.9	4.8	3.1	1.4	2.1	10.5

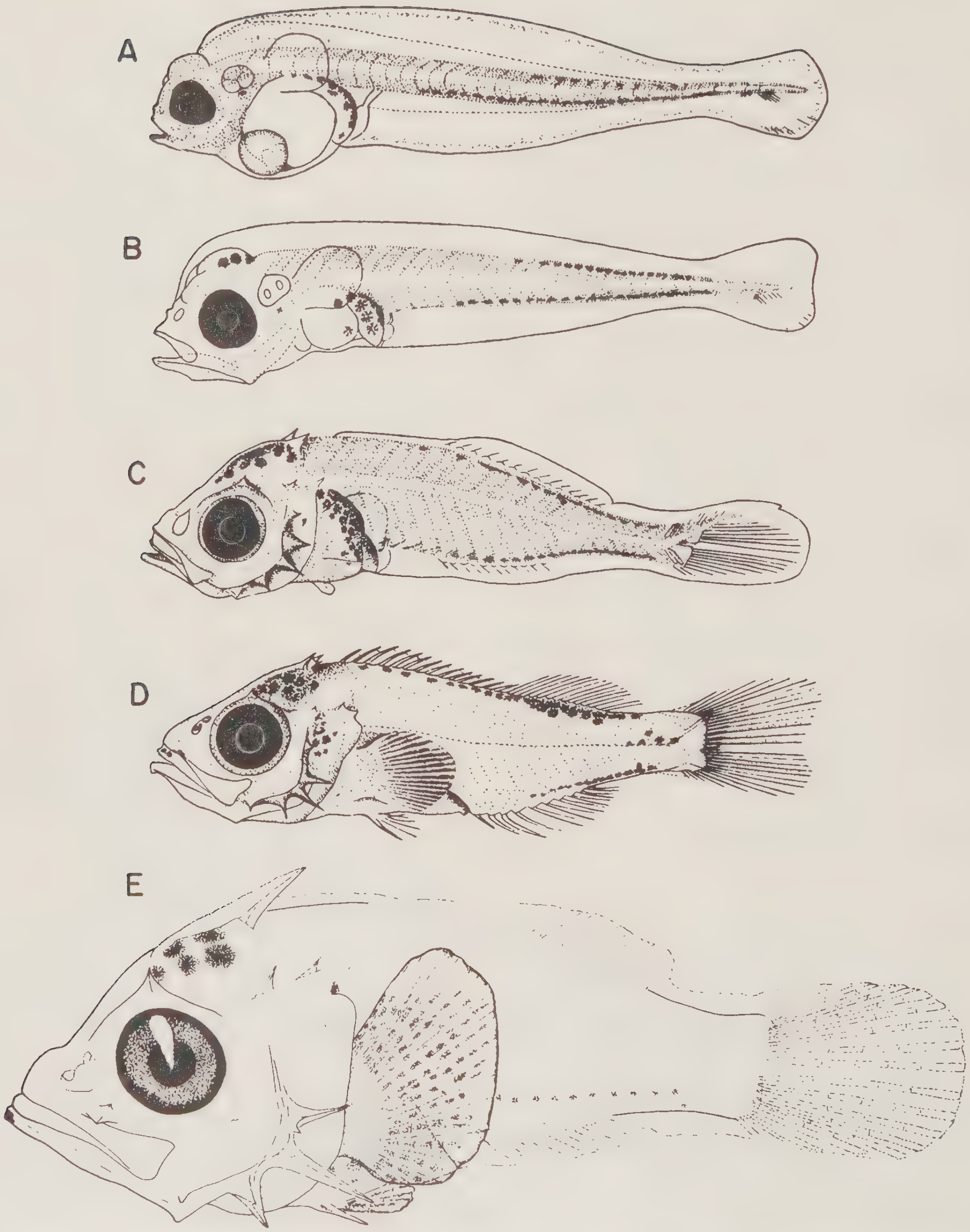

Figure 21.—Larvae of *Sebastes fasciatus* (A-D) from Bigelow and Welsh (1925) and a larva of *Sebastes capensis* (E). A. 6 mm; B. 9 mm; C. 12 mm; D. 20 mm; E. 7.2 mm.

the 7th to 14th (mean of 10.9 ± 1.35 for 111 specimens) postanal myomere and ended on the 14th to 22nd (mean of 19.1 ± 1.19 for 110 specimens) postanal myomere. In *S. marinus* the series began on the 10th to 15th (mean of 12.7 ± 1.41) postanal myomere and ended on the 18th to 22nd (mean of 20.3 ± 1.08) postanal myomere. In contrast to the ventral row in which the number of constituent melanophores is fixed during late intraovarian life, the dorsal row is gradually augmented before and after birth. The fact that the sample of *S. marinus* larvae was further advanced than any of the broods of *S. fasciatus* studied may account for the greater number of dorsal melanophores in the former. Consequently, a detailed study of comparable pre- and postnatal larvae of the two species would be necessary to evaluate the utility of this character in separating their larvae.

A well-known difference in the initial pigment pattern of the two larval types is the presence of one or more melanophores at the caudal region in *S. fasciatus* and the absence of caudal melanophores in most larvae of *S. marinus* (Templeman and Sandeman 1959). Caudal melanophores were present in all intraovarian larvae of *S. fasciatus* studied. The frequency was as follows: 40 larvae had 1 melanophore, 64 had 2, 14 had 3, and 2 had 4.

The subsequent development of pigment pattern in larvae of *S. fasciatus* is similar to that in *S. marinus*, although a number of differences are apparent. The ventral midline series becomes embedded gradually but some melanophores remain along each side of the base of the anal fin even in our largest larvae. In *S. marinus* larvae the developing anal fin obscures the ventral midline series and the remnants are visible only posterior to the fin in larvae longer than 11.8 mm. The dorsal midline series extends anteriad and splits into two lines with the developing dorsal fin between. The entire dorsum is spanned when the larvae are about 10.8 mm. In *S. marinus* larvae the entire dorsal midline is not spanned until the larvae reach about 15.0 mm.

The appearance of pigment characters at a smaller size (usually 1 to 3 mm smaller) in larvae of *S. fasciatus* compared with *S. marinus* larvae is a general developmental feature. For instance, pigment appears above the olfactory region of the brain in *S. fasciatus* larvae about 7.0 mm long and in *S. marinus* larvae about 9.3 mm long.

Another difference is the absence of certain pigment characters in *S. fasciatus* larvae and their presence in *S. marinus* of comparative size. Pigment does not appear on the isthmus, ventroposterior to the eye, and on the distal radials of the anal fin in *S. fasciatus* larvae of the size range studied, while in *S. marinus* larvae, these pigment features appear at about 15.7 mm. A more complete series of *S. fasciatus* larvae will be necessary to ascertain at what size these features appear or whether they appear at all.

Distribution.—Information on the geographic and bathymetric distributions of *S. fasciatus* is given by Templeman (1959).

Sebastes capensis (?) (Gmelin), Figure 21E

Literature.—Larvae of *Sebastes* from the Southern Hemisphere have not been previously described. The taxonomic status of this genus in the Southern Hemisphere is confusing, and Chen (1971) in his review of the subgenus *Sebastomus*, to which the southern forms belong, lumped the 11 nominal species into one. Eschmeyer and Hureau (1971) and Eschmeyer (pers. commun.), after examining specimens in South American museums, feel that there are at least three species off Chile. A total of 13 larval specimens from off Chile are available—five from the Marchile VI Expedition, six from Piquero IV, and two large specimens dip netted under a night-light in Valparaiso Harbor by Richard McGinnis of Pacific Lutheran University. Although some of these specimens are in poor condition and the series is incomplete, a brief description of them accompanied by an illustration serves as a basis for comparison with *Sebastes* from other regions of the world's oceans.

Distinguishing features.—Newborn larvae are small (about 3.8 mm), a feature which agrees with *Sebastes* larvae of the northeastern Pacific, and particularly the subgenus *Sebastomus* (Fig. 1). The larvae attain a large size, since the 19.6-mm dip net specimen is just beginning to transform.

Morphometric information on this species is incomplete because of the brevity of the developmental series (Table 24). The proportions generally follow those of other species, however, the depth of the pectoral fin base appears to be slightly greater in this species than in others measured, with a mean of 12.4% of the body length and a range of 8 to 17% for the seven larvae measured.

Pigmentation is similar to many of the *Sebastomus* species of the northeastern Pacific. Initially, the larvae have a spot above the nape, a spot on each side of the medulla, a group of melanophores at the symphysis of the lower jaw, a melanistic shield dorsolaterally on the gut, a group of melanophores on the ventral surface of the gut, and a series of melanophores along the ventral midline of the tail. The number of melanophores in the ventral midline ranged from 15 to 19 in four small larvae. The pectoral fins are distinctly pigmented with a group of melanophores on the medial surface of the fin base and melanophores distributed over the blade of the fin.

One or more melanophores lie above the optic lobes of the brain in larvae 4.6 mm and longer. As the pectoral fin

Table 24. Measurements (mm) of larvae of Sebastes capensis. (Specimens between dashed lines are undergoing notochord flexion.)

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-anal fin distance
3.8	1.5	0.80	0.19	0.35	0.85	0.33	0.32	---	---
4.6	1.8	1.1	0.36	0.43	1.2	---	---	---	---
5.5	2.6	1.8	0.60	0.59	1.7	0.62	0.72	0.05	---
6.2	2.8	1.9	---	---	1.8	0.77	0.75	0.06	3.7
7.0	3.7	2.3	0.83	0.93	2.6	1.3	1.1	0.28	4.3
7.2	4.0	2.7	0.93	0.94	2.7	1.3	1.2	0.65	4.3
14.8	8.9	5.6	1.5	1.7	5.5	3.8	1.7	2.5	9.4
19.6	12.0	7.1	2.1	2.1	6.9	5.3	2.0	3.7	12.8

rays differentiate, the melanophores become restricted to the interradial membrane and the distal margin of the pectoral fin develops a melanistic outline. The 7.2-mm larva has added a melanophore above the olfactory lobes, a spot on the ventrum at the juncture of the cleithra, and a covering of melanophores on the pelvic fins.

The gap in the series between 7.2 and 14.8 mm prevents study of pigment changes in this size range. The 14.8- and 19.6-mm specimens are pigmentless except for a wide band of melanophores on the caudal peduncle. Interestingly, many and possibly all species of *Sebastomus* from the northeast Pacific have a caudal peduncle band at this stage.

Fin counts on the two dip net specimens (dorsal, XIII, 13; anal, III, 6; pectoral, 18) fit known meristics for *S. capensis*. A count of 42 lateral line pores on the 19.6-mm specimen falls within the range for *S. capensis*.

Distribution.—Chen (1971) summarized the distributional information on this species.

Sebastes—Northwestern Pacific Species, Figure 22

Literature.—According to Chen (pers. commun.) there are 31 species of *Sebastes* in the northwestern Pacific. Life history series have been published on eight of these.

Fujita (1957) reared larvae of *S. pachycephalus nigricans* which had been extruded spontaneously by a captive pregnant female. The larvae were fed brine shrimp nauplii and kept at 16.4° to 18.8°C for 1 mo. The larval series was described and illustrated.

Fujita (1958) obtained a series of developing embryos of *S. oblongus* from two pregnant females maintained in an aquarium at 13.5° to 18.0°C. Larvae from one female were reared at 16° to 18°C on a diet of brine shrimp nauplii for 30 days until fin formation was completed. The series of developing embryos and larvae was described and illustrated.

Uchida et al. (1958) described and illustrated three specimens of *S. hubbsi* taken from plankton hauls.

Shiokawa and Tsukahara (1961) obtained a series of embryos of *S. pachycephalus pachycephalus* from captive females and then reared the larvae for 25 days at 15°C on a diet of brine shrimp nauplii. The embryos and larvae were described and illustrated as were demersal juveniles up to about 25-mm length netted from shallow water.

Harada (1962) described and illustrated a series of *S. inermis* that included late preextrusion larvae taken from pregnant females, larvae collected by plankton net, and juveniles up to about 60 mm in length.

Takai and Fukunaga (1971) followed development of embryos in a captive female of *S. longispinus* and reared the larvae for 30 days on a diet of brine shrimp and *Tigriopus* nauplii. The embryos and larvae were described and illustrated.

Sasaki (1974) removed late preextrusion larvae from freshly killed females of *S. schlegeli*, *S. steindachneri*, and *S. taczanowskii*. He summarized morphological and pigmentary characters of 20 specimens of each species and illustrated a specimen of each.

Distinguishing features.—Larvae of *S. oblongus* hatch at a total length of 7.25 mm or 6.5 mm notochordal length.[4] This is 1 mm larger than any eastern Pacific species described and slightly less than the range of *S. marinus* of the Atlantic. The most outstanding feature of *S. oblongus* larvae is the pattern of melanistic pigment, which begins to form well before hatching. Melanophores first appear as a shield over the dorsal surface of the gut, then patches form on the dorsal surface of the head, on the trunk above the gut, and as a band on the tail. At hatching, melanophores are continuous from the head to the broad tail band and they also appear on the ventral surface of the gut. The pectoral fins are unpigmented. With further development, pigment forms on the preopercular region of the head, along the jaws, the bases of the pectoral fins, and the tail band extends anteriorly and posteriorly. At notochord flexion the larvae are covered with melanophores except for the distal half of the pectoral fin blade and the caudal region (Fig. 22A). Larvae of *S. oblongus* differ from eastern Pacific and Atlantic species in their extraordinarily heavy pigmentation and in not developing the series of ventral midline melanophores on the tail.

Larvae of *S. longispinis* are spawned at about 5.3 to 5.5 mm notochordal length which is equivalent to *S. jordani*, the largest eastern Pacific species at hatching. Interestingly, the brood of *S. longispinis* studied by Takai and Fukunaga (1971) hatched as embryos within the ovary at about 3.1 mm notochordal length. Although this may have resulted from stress during captivity, it further strengthens the view that hatching occurs within the ovary in *Sebastes* and not after extrusion as stated by some authors (e.g., Morris 1956; Waldron 1968). The development of the pattern of melanistic pigmentation is almost identical to that in *S. oblongus* (Fig. 22B). The only difference appears to be in the absence of pigment on the distal portion of the pectoral fin base and on the blade of the fin.

Larvae of *S. hubbsi* represent a third member of this heavily pigmented group of Japanese *Sebastes*. The smallest of the three planktonic specimens described by Uchida et al. (1958) was a newborn larva 4.2 mm in notochordal length, indicating that larvae of this species are born at a length 1 mm smaller than larvae of *S. longispinis* and about 3 mm smaller than *S. oblongus*. The pigment pattern develops almost identically to that in the other two species, but differs chiefly in the sparse pigmentation of the pectoral fin base and in the development of evenly distributed minute melanophores on the blade of the pectoral fin (Fig. 22C).

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[4] It is customary in Japanese descriptions of fish larvae to give body length as total length, including the finfold. Since we use notochordal length in preflexion larvae, the total lengths were converted to notochordal length by measuring notochordal and total lengths on the illustrations and multiplying the resultant conversion factor by the actual total length given for the specimen.

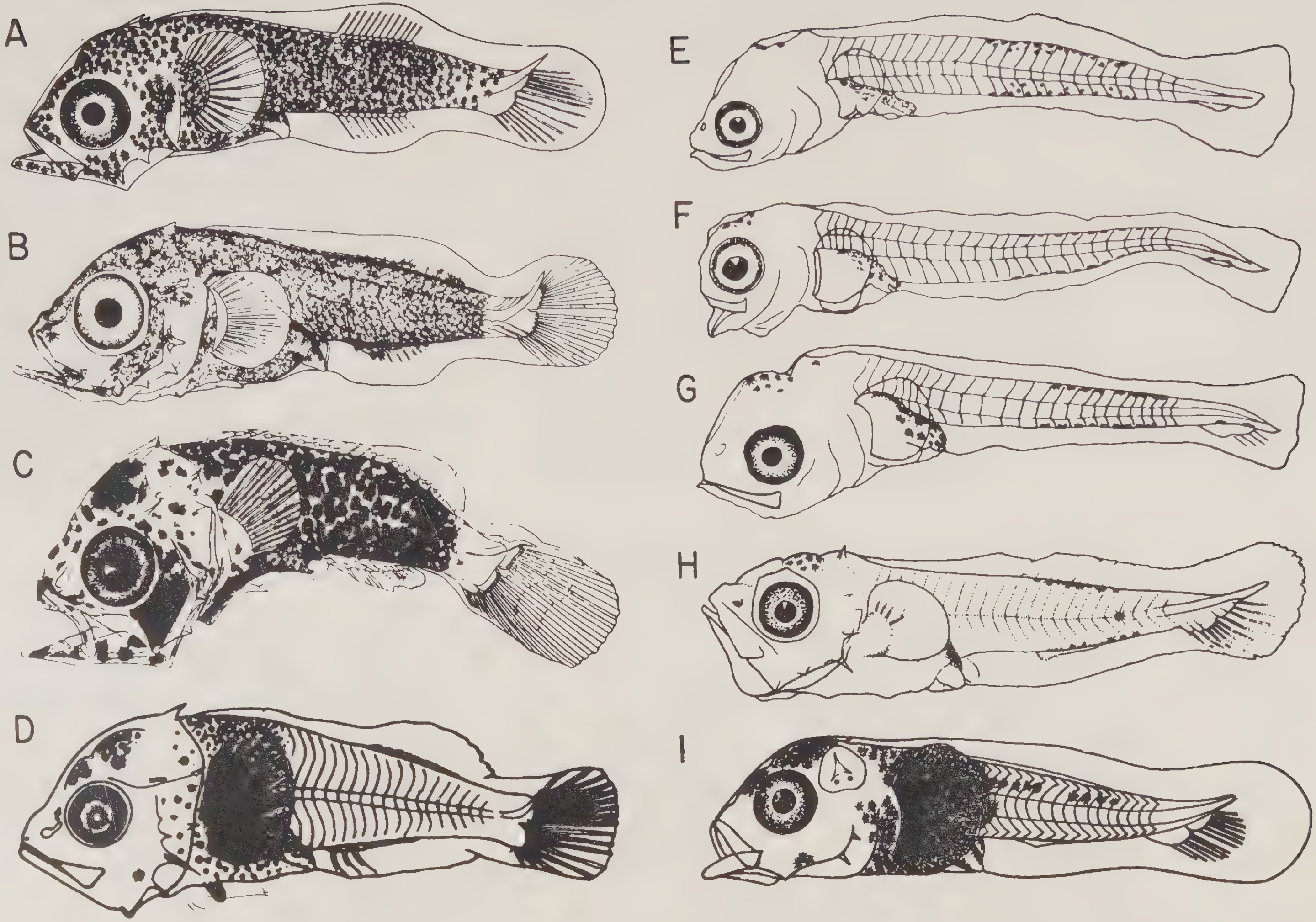

Figure 22.—Larvae of Japanese species of *Sebastes*. Measurements are total length. A. *S. oblongus*, 8.50 mm (from Fujita 1958); B. *S. longispinis*, 7.06 mm (from Takai and Fukunaga 1971); C. *S. hubbsi*, 6.03 mm (from Uchida et al. 1958); D. *S. pachycephalus pachycephalus*, 8 mm (from Shiokawa and Tsukahara 1961); E. *S. steindachneri*, 3.76 mm (from Sasaki 1974); F. *S. taczanowskii*, 4.50 mm (from Sasaki 1974); G. *S. schlegeli*, 5.69 mm (from Sasaki 1974); H. *S. inermis*, 7.1 mm (from Harada 1962); I. *S. pachycephalus nigricans*, 7.15 mm (from Fujita 1957).

A second type of *Sebastes* larva is represented by the subspecies *S. p. pachycephalus* and *S. p. nigricans*. Larvae of the two subspecies are extruded at lengths of 5.5 to 6.4 mm and 6.2 to 6.3 mm notochordal length, respectively, slightly larger than in eastern Pacific species. They also develop a striking pattern of melanophores. The first pigment to appear in embryos is a patch over the dorsal surface of the gut and a patch directly above this over the trunk. With further embryonic development, a large patch forms on the dorsal surface of the head and the base and blade of the pectoral fin is covered solidly with melanophores. As in the *S. oblongus* group, larvae of *S. pachycephalus* do not develop the series of ventral midline melanophores that is present in eastern Pacific and Atlantic *Sebastes*. At hatching, the heavy trunk band is augmented and melanophores have spread to the lateral and ventral surfaces of the gut. With further development, melanophores are added to the opercular region and the pectorals become solidly black.

The two subspecies differ in the pigmentation of the trunk and tail. Larvae of *S. p. pachycephalus* augment the anterior trunk band throughout larval development but develop no pigmentation on the posterior trunk and tail (Fig. 22D). Late in the larval period, two wide bands develop on the tail, one below the soft dorsal fin and one at the caudal peduncle. In preflexion larvae of *S. p. nigricans*, a line of melanophores extends posteriorly from the heavy trunk band to the caudal region (Fig. 22I). In later larval stages, melanophores are added to the lateral trunk and tail to form a continuous mass of pigment along the lateral body surface. The pelvic fins are solidly pigmented in both subspecies.

A third type of pigment pattern in Japanese *Sebastes* larvae is similar to that found in some species of the eastern Pacific and Atlantic. Late intraovarian larvae of *S. steindachneri* (Fig. 22E), *S. taczanowskii* (Fig. 22F), and *S. schlegeli* (Fig. 22G) all have a row of melanophores on the ventral midline of the tail, an opposing row along the dorsal midline, a patch on the dorsal surface of the brain, and a solid shield over the gut. They differ in the number of melanophores in each of the rows. Mean values for the number in the vental row of *S. steindachneri*, *S. taczanowskii*, and *S. schlegeli* are 16.3, 9.9, and 9.5, respectively, and for the dorsal row 18.7, 9.3, and 10.3, respectively. Size ranges in notochordal length for full-term larvae of the three species are 3.4 to 4.6 mm, 4.2 to 5.2 mm, and 4.8 to 6.8 mm, respectively.

A fourth species that falls into this group is *S. inermis*. Larvae are born at about 4 to 5 mm in length and Harada (1962) shows only dorsal head and gut pigment at this stage. His illustrations of 6- to 10-mm larvae show a short row of ventral and dorsal midline melanophores, but no numbers are given (Fig. 22H). No pectoral fin pigment is present on this species nor on the preceding three.

Helicolenus Goode and Bean

Literature.—Larvae of *Helicolenus dactylopterus* have been described and illustrated by a number of workers. Fage (1918) described a series of larvae 5.5 to 14 mm long from the Mediterranean Sea and illustrated the largest and smallest individuals of the series. Sparta (1942, 1956) described more completely the larval and early juvenile stages of *H. dactylopterus* from the Mediterranean and illustrated numerous larval stages and some juveniles. Haigh (1972) described the osteological development of a larval series from off South Africa. A series of excellent illustrations of *H. dactylopterus* are included with Tåning's (1961) description of redfish larvae from the North Atlantic.

Distinguishing features.—Larvae of *Helicolenus* can be differentiated from those of other scorpaenid genera by a combination of characters. Like *Sebastes*, larvae of *H. dactylopterus* have a small pectoral fin base (Table 3). Depth of the fin base averages 11% of the body length in larvae before notochord flexion, 12.5% during flexion, and 12% after flexion is completed. The range for the entire larval period is 9 to 14%. The blade of the fin is short and rounded. Fin length averages 11% of the body length in preflexion larvae, 15% during flexion, and 18% following flexion. Another distinctive feature is the mass of spongy tissue which forms at the dorsal midline of the trunk. It appears within the dorsal finfold in 4-mm larvae in the region to be occupied by the spinous dorsal fin. In later stages the spinous dorsal rays form within the mass and erupt from it. Such tissue has not been described for larvae of any other scorpaenid genus.

Larvae of the species of *Helicolenus* from the eastern Pacific off Chile, *H. lengerichi*, were not available for study. For comparative purposes, a brief description of a series of the North Atlantic species, *H. dactylopterus*, is given below and accompanied by the illustrations of Poul Winther (Tåning 1961).

Helicolenus dactylopterus (Delaroche), Figure 23

Literature.—See above.

Distinguishing features.—Planktonic eggs of *H. dactylopterus* have not been described, and there is uncertainty about the mode of reproduction of this species. Krefft (1961) reported that ovaries of reproductively mature females contained developing embryos embedded in a gelatinous matrix. Thus, *Helicolenus* may be ovoviviparous as in the subfamily Sebastinae or may produce a gelatinous egg balloon as in many genera of the Scorpaeninae. Krefft (pers. commun.) has suggested that the ovoviviparity may be facultative. Larvae are small at hatching as in the Scorpaeninae; Sparta (1942) illustrated a 2.8-mm larva that has already utilized its yolk and is morphologically similar to *Scorpaena* larvae of that size.

Body depth is moderate and increases throughout the larval period, from an average of 29% of the body length in preflexion larvae, to 33% in larvae undergoing flexion, to 37% in postflexion larvae (Table 25). The gut is compact. Snout-anus distance averages 49% of the body

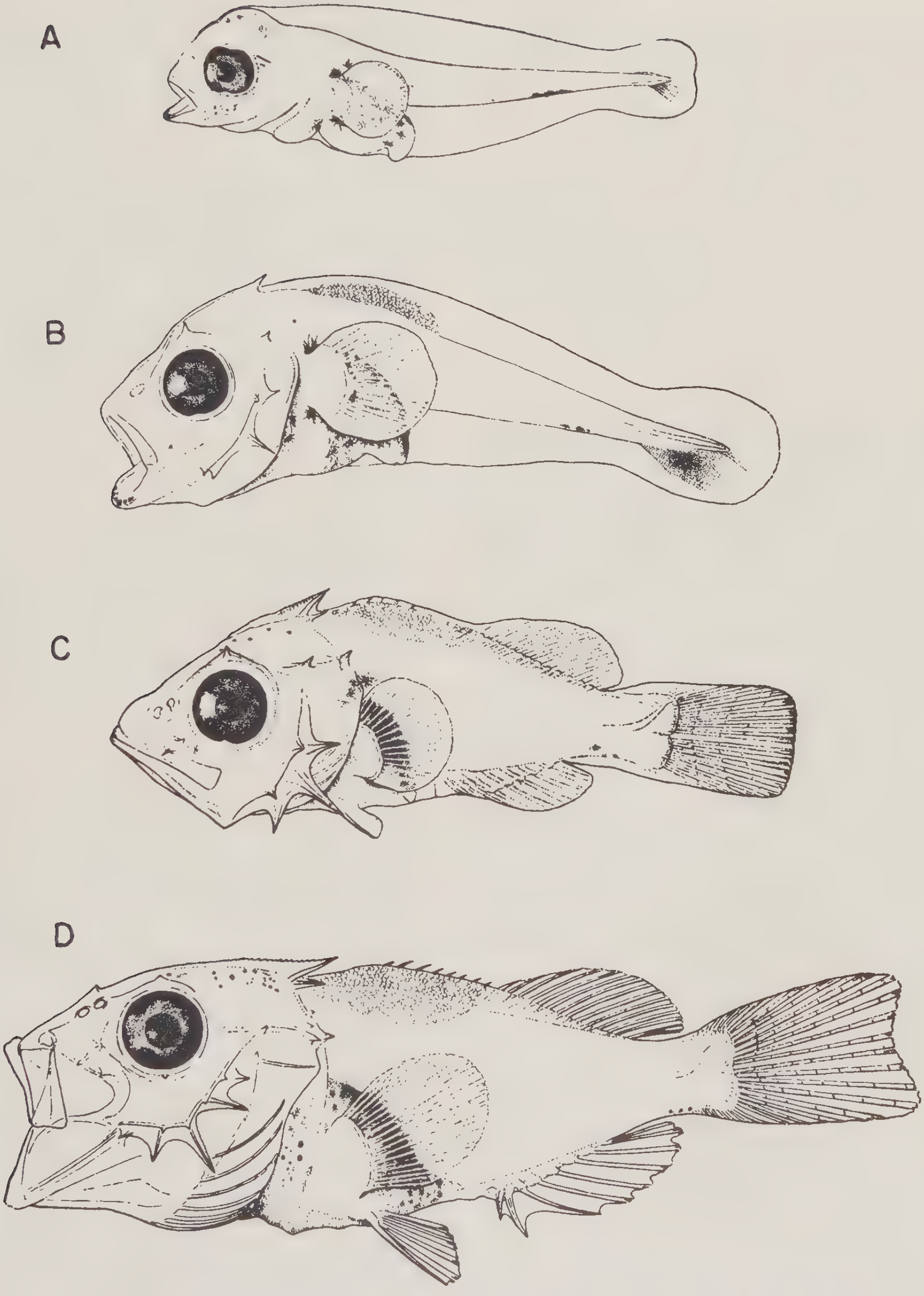

Figure 23.—Larvae of *Helicolenus dactylopterus* from Táning (1961). A. 3.6 mm; B. 5.6 mm; C. 10.0 mm; D. 19.0 mm.

Table 25. Measurements (mm) of larvae of *Helicolenus dactylopterus*. (Specimens between dashed lines are undergoing notochord flexion.)

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-anal fin distance
3.2	1.5	0.95	0.28	0.29	0.81	0.34	0.35	---	--
3.8	1.8	1.2	0.45	0.35	1.2	0.40	0.35	--	
4.6	2.3	1.6	0.53	0.43	1.3	0.52	0.55	---	---
5.0	2.6	1.7	0.63	0.47	1.4	0.60	0.60	-	-
5.9	2.8	1.9	0.62	0.58	1.8	0.71	0.65	0.04	3.5
6.0	3.0	2.2	0.82	0.63	2.0	0.80	0.69	0.08	3.6
6.2	3.0	2.1	0.82	0.62	1.9	0.90	0.74	0.10	3.6
6.6	3.1	2.3	0.80	0.65	2.2	0.92	0.79	0.14	3.8
6.8	3.4	2.4	0.96	0.74	2.3	1.1	0.90	0.15	4.0
6.9	3.3	2.4	0.92	0.77	2.3	1.1	0.92	0.15	4.0
7.9	4.3	3.0	1.1	0.78	2.7	1.2	1.0	0.32	5.2
8.1	4.7	3.1	1.2	1.0	2.8	1.3	1.1	0.50	5.0
8.6	4.8	3.5	1.2	1.0	3.2	1.5	1.2	0.70	5.4
9.8	5.8	3.9	1.2	1.2	3.6	1.7	1.2	1.1	6.2
10.7	6.2	4.1	1.3	1.3	4.1	2.1	1.3	1.2	6.7
15.4	9.1	6.2	2.2	1.7	5.6	3.1	1.6	2.1	9.6

length in larvae up to notochord flexion and thereafter increases to an average of 58%. Head length also increases during the larval period from an average of 35% of body length in preflexion larvae, to 36% in larvae undergoing flexion, to 37% in postflexion larvae. The eye is moderate in size and averages 30% of the head length during the larval period with no trend of relative increase. Snout length averages 35% of the head length over the larval period.

The bases and blades of the pectoral fins are well differentiated in the 2.8-mm specimen of Sparta (1942). The short round blade portion of the pectoral fin is another feature held in common with many species of *Sebastes*. The paucity of specimens of *H. dactylopterus* precluded staining for osteological study; however, the size at formation of pectoral fin rays can be observed in unstained specimens. Pectoral rays begin to appear when the larvae are about 4.0 mm long and the last (lowermost) rays have differentiated at about 8.0 mm. The usual number of rays is 19. The pelvic fin buds appear in larvae about 6.0 mm long. The rays begin differentiating in 7-mm larvae, and the full complement of one spine and five rays is present in the 8.6-mm specimen.

The hypural anlage of the caudal fin is apparent in 3-mm larvae and the elements and principal caudal rays begin to differentiate in 4-mm larvae. The full complement of principal rays (8 + 7) is present in 7-mm larvae. Notochord flexion occurs at a relatively large size (6.0 to 8.0 mm) as in *Sebastes* and is another character held in common by the two genera. The dorsal and anal fins begin to form simultaneously in larvae about 6.0 mm long, but the full complements of XII, 11 or 12 dorsal rays and III, 5 anal rays are not present until 8.6 mm.

Larvae of *H. dactylopterus* have a distinctive pigment pattern that is established in larvae less than 3.0 mm long. On the head, a group of melanophores is present on the lower jaw and above the brain. The dorsolateral surfaces of the gut are covered with a solid shield of pigment which enlarges ventrally with continued development. Several superficial melanophores are present on the trunk just above the axillary region. The medial surface of the pectoral fin base is solidly pigmented and fine melanophores are located at two regions on the blade of the fin, some near the distal margin and another group at the basal region of the fin blade. A group of melanophores is present at the ventral midline of the tail just anterior to where the caudal fin will form. This unique pattern of pigmentation remains essentially unchanged throughout the entire larval period.

Distribution.—Adults of *H. dactylopterus* have a complex distribution. Eschmeyer (1969) recognized two Atlantic subspecies, *H. d. dactylopterus* and *H. d. lahillei*, with the former composed of four separate populations (northeastern Atlantic and Mediterranean, Gulf of Guinea, South Africa, and northwestern Atlantic). The subspecies *H. d. lahillei* is found off Uruguay and Argentina. The 6.0- and 6.2-mm specimens in the series are from *Discovery* station 714, off Uruguay, and thus are larvae of *H. d. lahillei*. They are not distinguishable from larvae of *H. d. dactylopterus*.

Sebastolobus Gill

Literature.—Pearcy (1962) described the floating egg masses, the developing embryos, and the newly hatched larvae of *Sebastolobus*. The larvae, pelagic juveniles, and early demersal juveniles of *S. altivelis* and *S. alascanus* are described and illustrated in Moser (1974). Larvae of the other species in the genus, *S. macrochir*, of the northwestern Pacific, have not been described; however, pelagic juveniles of this species are described and illustrated in Moser (1974).

Distinguishing features.—Early *Sebastolobus* larvae (up to 6 mm) can be distinguished from those of all other genera of eastern Pacific Scorpaenidae on the basis of pigmentation. *Sebastolobus* larvae of this size range are unique in having two large melanistic blotches about midway along the tail, one at the dorsal midline and one at the ventral midline. These are sometimes expanded to form a solid band on the tail (Fig. 24). Early larvae of all other eastern Pacific scorpaenid genera have a series of melanophores along the ventral midline of the tail, and in some species of *Sebastes*, an opposing row is present at the dorsal midline. The large tail blotches of *Sebastolobus* disappear in larvae between 4.2 and 6.4 mm. Soon after the loss of these large tail blotches the larvae develop prominent crestlike parietal ridges that terminate in double spines, the posterior (nuchal) spine being longer and more prominent than the anterior (parietal) spine (Fig. 24). Of the other eastern Pacific scorpaenid genera, only the larvae of *Scorpaenodes* have parietal ridges and spines like *Sebastolobus*. If two spines are present on the parietal ridges of other genera, the anterior spine is always longer and more prominent than the posterior. *Sebastolobus* larvae may be distinguished from those of *Scorpaenodes* on the basis of a melanistic shield, which covers the dorsolateral surface of the gut in the former and is absent in the latter. Larvae of *Sebastolobus* smaller than 10.0 mm could not be identified to species. Larvae larger than this can be identified to species by a combination of characters that are

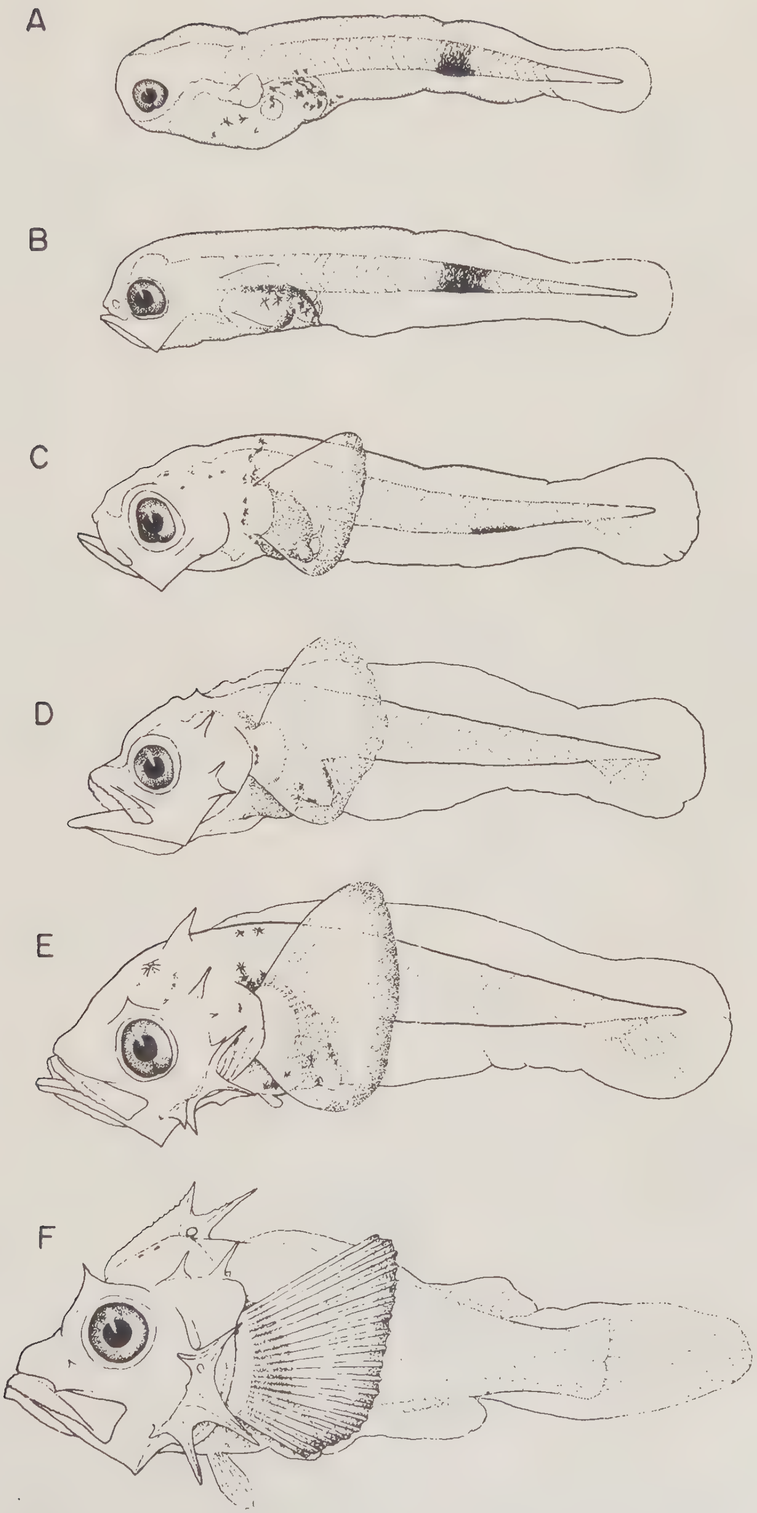

Figure 24.—Larvae of *Sebastolobus* spp. A. 3.0 mm; B. 3.5 mm; C. 5.2 mm; D. 5.7 mm; E. 6.2 mm; F. 7.7 mm.

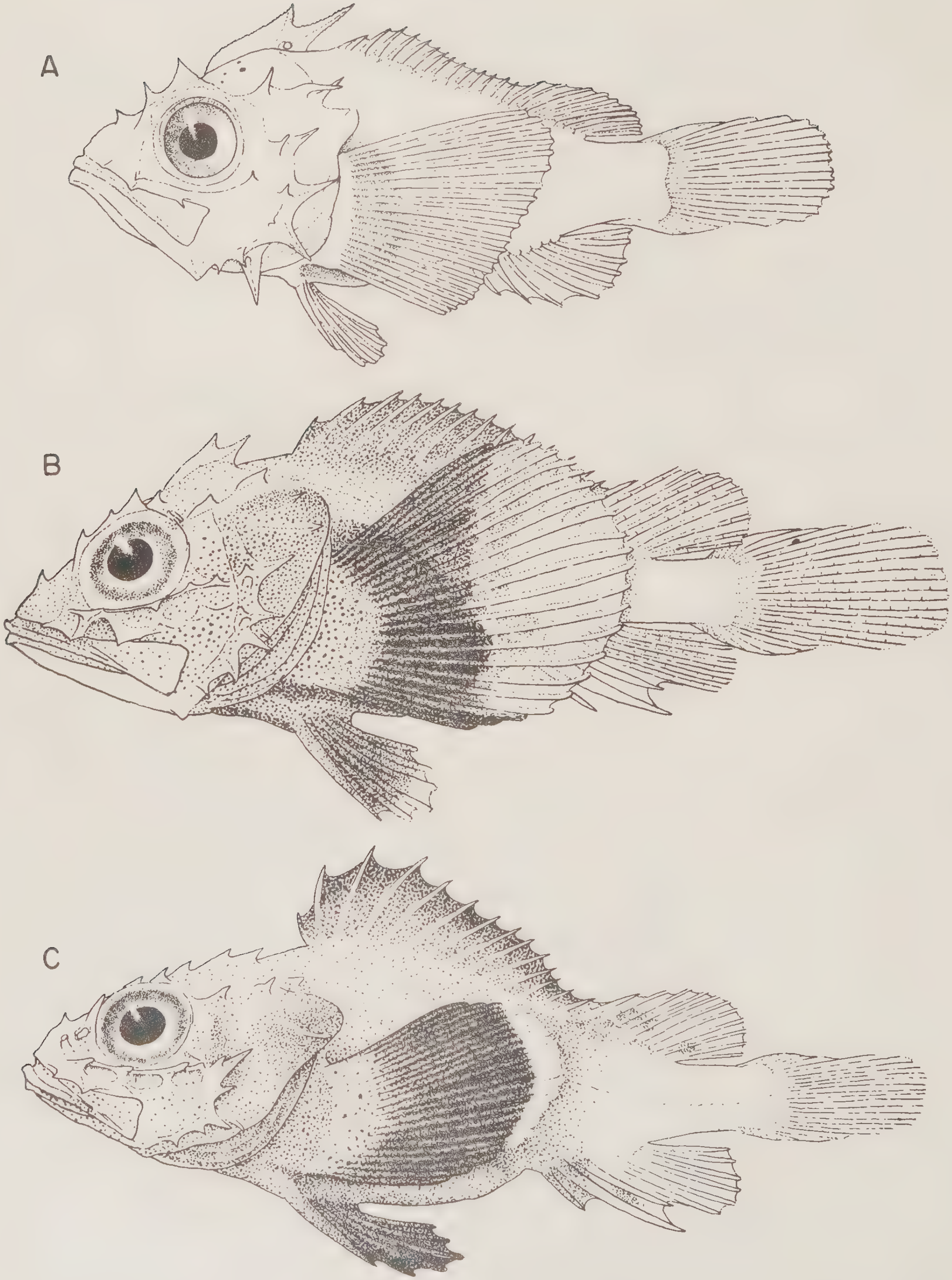

Figure 25.—Developmental series of *Sebastolobus altivelis*. A. 11.2-mm larva; B. 26.8-mm pelagic juvenile; C. 53.5-mm pelagic juvenile.

given in the following species descriptions of *S. altivelis* and *S. alascanus*.

***Sebastolobus altivelis* Gilbert, Figure 25**

Literature.—Larvae, pelagic juveniles, and early demersal juveniles are described in Moser (1974).

Distinguishing features.—Larvae of *Sebastolobus* hatch and are freed from their floating egg mass at about 2.6 mm in length. They have an elliptical yolk sac with a posteriorly positioned oil droplet. When the larvae reach approximately 3.5 mm, the yolk sac has been resorbed and the jaws and feeding apparatus are well formed. Flexion of the notochord begins in larvae about 6.0 mm long and is completed in larvae about 7.5 mm (Table 26). Transformation into the pelagic juvenile stage is initiated within the size range of 14.0 to 20.0 mm (Table 27). All specimens larger than 20.0 mm have some juvenile pigmentation. The pelagic juvenile stage of *S. altivelis* is highly protracted and may last as long as 20 mo. Transformation into demersal juveniles occurs within the size range of about 42 to 56 mm.

Larvae larger than 10 mm may be differentiated to species on the basis of body depth and pectoral fin shape. Larvae and transforming specimens of *S. altivelis* are more robust and deeper-bodied than those of *S. alascanus*. Body depth of specimens of *S. altivelis* in the 10- to 20-mm size range is 36 to 45% of the body length (mean of 41%), whereas in specimens of *S. alascanus* of comparable size the range is 33 to 39% with a mean of 35%. The pelagic juveniles of *S. altivelis* are equally robust; body depth averages 41% of body length in the 20- to 40-mm size range but then decreases gradually to 34% in the largest pelagic juveniles. Pelagic juveniles of *S. alascanus* are less robust; body depth averages 34% with a range of 31 to 36%.

As in other scorpaenid genera, the pectoral fins provide excellent characters for species separation. The pectorals are longer and have a deeper base in larvae and pelagic juveniles of *S. altivelis* compared with *S. alascanus*. In specimens of *S. altivelis* in the 10- to 20-mm size range, the pectoral fin length averages 34% of the body length (range of 29 to 39%). The pectorals reach their maximum relative length in 20- to 40-mm pelagic juveniles where they average 39% of the body length (range of 35 to 41%). In pelagic juveniles 40 to 50 mm long the average is 35% (range of 32 to 37%). In 10- to 27-mm specimens of *S. alascanus* fin length averages 29% of body length (range of 26 to 31%).

The two species can be separated by a combination of meristic characters. *Sebastolobus altivelis* usually has one or two more pectoral fin rays and one or two less vertebrae than *S. alascanus* (Table 28).

The melanophore pattern of larvae of *S. altivelis* is indistinguishable from that of *S. alascanus*. At the beginning of the larval stage (3.5 mm) there are large median blotches opposite each other about midway back on the tail. In some specimens, the blotches are expanded to form a band. Also, melanophores cover the dorsolateral surfaces of the posterior region of the gut. The melanistic tail blotches are transitory; they are lost in some larvae as small as 4.2 mm and one or both are absent in most larvae between 5.0 and 6.0 mm in length. The dorsal blotch was absent in all larvae larger than 6.0 mm and the ventral one was absent in all larger than 6.4 mm. In contrast, the gut pigment is augmented throughout the larval period, extending forward to the axillary region and internally anterior to the cleithrum in larvae about 5.0 mm long. When the larvae reach 6.0 mm, the pigment extends onto the ventral surface of the gut and dor-

Table 26. Measurements (mm) of Sebastolobus spp. larvae. (Specimens between dashed lines are undergoing notochord flexion.)

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-dorsal fin	Snout-anal fin
3.0	1.3	0.50	0.08	0.20	0.60	0.3	0.14			
3.5	1.4	0.80	0.18	0.25	0.52	0.23	0.20			
3.8	1.6	1.0	0.22	0.27	0.68	0.40	0.38			
4.2	1.8	1.2	0.25	0.30	0.86	0.45	0.40			
4.7	1.9	1.2	0.31	0.30	0.80	0.46	-			
5.0	2.0	1.4	0.35	0.33	0.90	0.65	0.50			
5.2	2.1	1.4	0.43	0.40	1.0	0.62	0.55			
5.5	2.3	1.6	0.42	0.35	1.1	0.65	0.58			
5.7	2.3	1.7	0.56	0.40	1.2	0.95	0.85			
5.8	2.4	1.7	0.51	0.39	1.2	1.0	0.78			
5.9	2.6	1.8	0.62	0.47	1.6	1.0	0.75			
6.0	2.7	1.8	0.55	0.51	1.8	1.3	0.85	0.22	2.3	3.4
6.2	2.7	1.9	0.70	0.48	1.6	1.4	0.90	0.20	-	-
6.4	2.7	1.8	0.60	0.45	1.5	1.2	0.85	0.13	-	-
6.7	3.1	1.9	0.82	0.55	1.8	1.4	1.0	0.15	3.9	3.9
6.8	2.8	2.0	0.82	0.52	1.8	1.4	1.1	0.17	-	3.2
6.9	3.3	2.2	0.80	0.58	2.0	1.5	1.2	0.25	2.7	4.1
7.1	3.5	2.5	0.82	0.71	2.4	1.8	1.2	0.80	2.5	4.2
7.3	3.8	2.5	0.95	0.76	2.4	1.8	1.4	0.85	2.7	4.4
7.7	4.2	2.7	1.1	0.75	2.8	2.1	1.5	0.85	2.9	4.5
7.8	4.3	3.1	1.1	0.82	2.6	2.1	1.4	1.2	3.2	4.8
8.3	4.4	3.1	1.1	0.79	2.6	2.0	1.4	1.0	3.1	4.9
8.6	4.8	3.2	1.2	0.92	3.1	2.4	1.7	1.4	3.5	5.3
8.9	5.2	3.3	1.2	1.0	3.1	2.5	1.7	1.4	3.8	5.4
9.2	5.2	3.5	1.2	1.0	3.2	2.7	1.5	1.5	3.8	5.6
9.6	5.4	3.5	1.2	1.1	3.7	2.8	1.8	1.7	4.1	5.8

Table 27. Measurements (mm) of Sebastolobus altivelis. (Specimens below dashed line have completed transformation into pelagic juvenile stage.)

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-dorsal fin	Snout-anal fin
10.1	6.2	3.8	1.2	1.2	3.8	2.8	1.8	1.7	4.2	6.4
10.5	6.5	4.2	-	1.2	3.9	3.0	1.9	1.8	4.4	6.7
11.2	6.9	4.5	1.3	1.4	4.2	3.5	2.1	2.4	5.2	7.3
12.7	7.3	4.6	1.3	1.5	4.7	3.8	2.0	2.5	5.4	7.9
13.4	8.0	5.0	1.5	1.6	4.8	3.7	2.0	2.5	5.4	8.3
14.4	8.8	6.2	1.7	2.1	5.7	5.0	2.7	3.1	6.0	9.6
15.2	10.1	6.1	1.8	1.9	6.3	5.2	2.8	2.9	6.7	10.6
15.4	9.8	6.0	1.7	2.2	6.4	4.7	2.8	2.9	6.9	10.1
15.4	9.9	6.5	1.9	2.2	6.3	5.8	2.9	3.8	6.8	11.0
15.7	10.3	6.8	2.1	2.1	6.9	5.8	2.9	3.8	6.7	10.8
16.0	10.3	6.2	1.8	2.0	7.1	5.4	3.1	3.3	7.0	10.6
16.3	10.3	7.2	2.1	2.2	6.6	6.2	3.0	4.0	6.8	11.2
16.6	10.8	7.4	1.8	2.4	6.6	6.4	3.0	3.4	7.6	11.8
16.7	11.2	6.7	1.9	2.2	7.5	5.8	3.2	3.3	7.1	11.3
17.6	11.5	7.6	2.0	2.5	7.2	6.8	3.2	4.2	7.1	12.2
17.6	11.7	7.0	1.9	2.4	7.3	5.9	3.1	3.8	7.7	12.0
18.2	12.0	7.7	2.1	2.6	7.3	6.3	3.1	4.2	7.8	12.7
18.4	12.5	7.1	2.0	2.5	8.3	6.2	3.6	4.2	7.5	12.8
19.3	13.2	7.9	2.1	2.5	8.5	6.7	3.8	3.8	8.3	13.4
19.4	13.0	8.5	2.3	2.5	8.7	7.6	3.8	4.7	8.4	14.0
20.7	13.8	8.5	2.6	2.3	8.4	7.6	3.7	4.8	8.6	14.7
21.3	14.9	9.2	2.8	2.8	9.0	8.1	3.8	4.8	9.5	15.2
22.6	15.9	9.6	2.5	3.1	9.2	8.8	4.2	5.6	9.5	16.7
23.4	16.6	9.8	2.5	2.7	10.1	9.0	4.4	5.6	9.5	17.4
24.5	17.7	10.8	2.9	3.4	11.0	10.0	4.5	5.8	10.1	18.1
25.8	18.6	10.6	2.9	2.9	11.3	9.3	4.4	5.9	10.1	18.9
26.8	17.7	10.6	2.8	3.8	10.6	11.0	4.8	6.5	10.1	18.8
27.7	20.3	11.5	2.9	3.6	12.2	11.0	5.4	7.1	11.7	22.0
28.3	20.3	12.0	3.2	3.7	12.2	11.5	5.0	7.1	11.5	21.8
29.4	20.4	12.3	3.3	3.8	11.5	11.5	5.2	7.2	12.3	21.1
30.5	21.1	13.0	3.8	3.6	11.7	11.7	5.4	7.6	12.3	23.0
31.4	21.1	12.3	3.2	3.5	13.7	12.2	5.8	7.5	12.3	22.9
32.4	21.1	12.5	3.5	3.6	13.0	12.8	5.8	8.3	12.5	22.2
33.6	23.1	14.0	4.2	4.2	13.5	11.7	5.8	7.5	12.8	25.1
34.6	23.5	13.4	3.8	3.8	14.2	13.5	6.0	8.2	13.7	25.5
36.5	25.0	15.2	4.2	4.8	15.5	14.7	6.7	9.2	14.9	27.5
37.5	25.8	15.0	4.2	4.6	15.9	14.4	6.7	8.3	14.7	27.6
38.5	25.6	15.2	4.0	4.8	16.0	15.7	6.6	9.8	15.2	27.5
39.5	27.9	16.2	5.0	4.8	16.0	15.0	6.7	8.9	16.0	29.9
40.4	27.1	16.4	5.0	4.8	15.2	15.0	6.8	10.8	16.0	30.0
41.6	27.9	16.4	4.3	5.8	15.9	15.2	7.1	10.1	16.2	29.6
42.3	28.1	16.9	4.6	5.2	17.4	15.2	7.2	10.0	15.9	29.4
43.5	30.1	16.9	5.2	5.4	16.0	14.7	6.7	9.5	17.4	32.4
44.4	30.0	17.9	-	4.8	16.4	16.4	7.1	9.5	17.2	32.2
45.1	29.5	18.2	4.8	5.4	17.6	16.0	7.8	10.1	17.2	32.0
46.2	30.7	17.9	5.0	4.9	17.7	17.1	8.1	11.5	17.1	33.5
47.1	30.2	18.1	5.0	5.6	17.1	15.2	7.0	10.3	17.7	33.0
48.5	32.0	18.6	5.4	5.8	18.6	16.9	7.8	10.5	17.7	34.7
49.5	32.2	19.8	5.0	5.8	18.6	18.1	8.3	11.8	16.4	36.2
51.3	37.0	20.6	6.7	5.8	18.8	17.4	8.0	11.3	18.9	40.0
53.5	35.7	20.6	6.2	7.5	18.6	16.9	8.2	11.0	18.7	37.8
56.0	37.6	21.4	5.8	7.7	19.2	19.8	8.3	12.3	20.3	40.6
*42.0	26.8	16.6	4.6	5.6	12.0	12.7	6.0	9.3	16.4	29.0
*47.4	29.6	17.7	4.7	6.9	13.9	13.5	6.8	10.1	18.1	31.7
*48.1	31.4	19.1	5.2	7.3	14.4	15.2	7.0	11.5	17.9	33.5
*50.3	33.0	19.2	5.4	7.3	14.0	13.8	7.1	11.8	18.8	35.3
*51.0	33.0	19.5	4.7	7.2	15.0	16.2	7.5	11.2	18.7	35.2
*53.0	33.4	20.5	5.4	8.6	14.6	15.5	7.0	12.1	19.9	37.7
*54.0	35.4	19.7	5.9	7.3	15.5	17.7	7.8	12.6	20.6	38.4
*56.0	35.2	21.1	5.6	7.7	15.5	16.4	7.4	12.6	20.8	38.1
*57.5	37.2	21.4	5.6	8.0	15.3	16.7	8.1	12.5	21.1	40.3
*58.6	37.9	22.6	6.0	8.7	16.5	16.9	8.2	12.7	21.6	40.6
*60.0	38.0	22.0	6.0	8.4	16.2	15.1	8.1	12.8	21.5	41.6

*Benthic juvenile.

Table 28. **Meristics from cleared and stained larvae and juveniles of *Sebastolobus* spp. (above dashed line) and *Sebastolobus altivelis* (below dashed line).**

Length (mm)	Primary caudal fin rays		Secondary caudal fin rays		Branchio-stegal rays		Pectoral fin rays		Hypural elements		Gill rakers (right arch)		Anal fin rays	Dorsal fin rays	Pelvic fin rays		Vertebrae
	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right	Superior	Inferior	Upper limb	Lower limb			Left	Right	
6.2	-	-	-	-	5	5	-	-	-	-	-	-	-	-	-	-	-
6.8	-	-	-	-	3	3	14	2	-	-	-	3	-	-	-	-	-
7.0	8	7	-	-	5	5	14	12	-	-	-	2	-	-	-	-	-
7.7	8	7	4	4	7	7	23	24	2	1	3	9	III-5	XV-9	I-5	I-5	28
8.1	8	7	-	2	7	7	23	23	-	-	3	9	III-3	XV-9	I-5	I-5	28
8.3	8	7	3	4	7	7	23	23	2	1	2	8	III-5	XV-9	I-5	I-5	27
8.8	8	7	4	5	7	7	23	24	2	2	3	10	III-5	XV-9	I-5	I-5	29
9.3	8	7	3	4	7	7	24	24	2	1	3	10	III-5	XV-9	I-5	I-5	29
10.1	8	7	6	8	7	7	23	23	1	2	5	12	III-5	XV-9	I-5	I-5	29
10.6	7	7	6	7	7	7	23	23	1	2	5	13	III-6	XV-10	I-5	I-5	29
11.2	8	7	6	7	7	7	23	23	1	2	5	13	III-5	XV-9	I-5	I-5	28
11.5	8	7	7	7	7	7	23	23	1	2	5	13	III-5	XV-9	I-5	I-5	29
12.0	8	7	6	7	7	7	23	23	2	2	5	13	III-5	XV-8	I-5	I-5	28
13.0	8	7	6	7	7	7	23	24	2	2	6	13	III-5	XV-10	I-5	I-5	29
13.7	8	7	6	7	7	7	23	23	2	2	5	13	III-5	XV-9	I-5	I-5	29
14.4	8	7	7	7	7	7	23	24	2	2	6	14	III-5	XV-9	I-5	I-5	29
15.0	8	7	7	7	7	7	23	23	2	2	6	13	III-5	XV-9	I-5	I-5	29
16.6	8	7	7	7	7	7	23	23	2	2	7	14	III-5	XV-9	I-5	I-5	29
17.6	8	7	8	7	7	7	23	23	2	2	7	14	III-5	XV-9	I-5	I-5	29
18.1	8	7	7	7	7	7	24	23	2	2	7	14	III-5	XV-9	I-5	I-5	29
19.4	8	7	7	7	7	7	22	22	2	2	6	14	III-5	XV-9	I-5	I-5	29
20.6	8	7	8	8	7	7	23	23	2	2	7	14	III-5	XV-9	I-5	I-5	29
25.8	8	7	8	9	7	7	24	23	2	2	6	15	III-5	XV-9	I-5	I-5	29
30.5	8	7	6	7	7	7	24	24	2	2	7	15	III-5	XVI-9	I-5	I-5	29
40.4	8	7	7	7	7	7	23	23	2	2	7	15	III-5	XV-9	I-5	I-5	29
50.0	8	7	7	7	7	7	23	23	2	2	7	14	III-5	XV-8	I-5	I-5	29

sally as deeply embedded pigment at the nape. With continued development the melanophores form a solid sheath on the peritoneum surrounding the gut.

Melanophores appear at the posterior margin of each pectoral fin in some larvae as small as 4.0 mm. About half the larvae examined between 4.0 and 5.0 mm have this posterior margin of fine melanophores and the pigment is present in all larvae in the 5.0- to 11.0-mm range. The melanophores are then lost, and almost all larvae larger than 11.0 mm have unpigmented fins.

Melanophores appear on the posterior lobes of the brain in 5.2- to 7.0-mm larvae and are present in all larvae larger than this. They also appear above the anterior lobes of the brain in larvae between 7.0 and 9.0 mm in length and in most larvae larger than 9.0 mm.

Pigmentation of the pelagic juveniles of the two species is markedly different. It begins to appear in some specimens of *S. altivelis* of the 14- to 20-mm size range. On the head, patches of melanophores appear on the opercle, cheek, snout, and jaws. In most specimens larger than 22 mm, the patches are confluent, and the head is generally dusky with darker areas at the opercle and along the upper jaw.

A patch of melanophores appears superficially over each side of the gut in specimens as small as 14 mm. These patches expand to form a solid melanistic sheath in some specimens of the 14- to 20-mm size range. The posterior margin of the sheath is an arc running from the vent to the nape and stands out sharply against the pigmentless region of the trunk posterior to the sheath. With continued development the pigment sheath expands posteriad and is a striking feature of the pelagic juveniles. In the 20- to 30-mm size range the sheath extends posteriad to a vertical from the first or second anal fin spines. In the 30- to 40-mm size range the sheath extends posteriad to the 2nd or 3rd anal spine in most specimens and to the soft dorsal fin in some. In most pelagic juveniles of the 40- to 50-mm size range, the dusky sheath extends back to the soft dorsal and it does so in all specimens of the 50- to 60-mm size range. When the juveniles become benthic, the dusky sheath extends posteriad to the caudal fin.

The fins become deeply and characteristically pigmented in juveniles of *S. altivelis*. The anterior portion of the spinous dorsal fin becomes melanistic in specimens as small as 18 mm. In juveniles of the 20- to 25-mm size range, the anterior one-half to two-thirds of the fin is melanistic. In the 25- to 30-mm range, three-fourths or more of the fin is black. In pelagic juveniles larger than this the pigment has spread onto the soft dorsal fin, and covers both the soft dorsal and soft anal fins in benthic juveniles.

The base of the pectoral fins begins to be covered with melanophores in specimens as small as 14 mm. In specimens as small as 18 mm the melanophores extend onto the basal region of the rays. With further growth the black basal zone enlarges posteriad and becomes a highly characteristic feature of the pelagic juveniles. The posterior margin of this zone contrasts sharply with the distal clear region of the fin. In juveniles of the 19- to 25-mm size range, the width of the black basal zone averaged 20% of the fin length. Enlargement of this zone is shown by the average relative widths for successive size ranges (25 to 30 mm, 38%; 30 to 35 mm, 46%; 35 to 40 mm, 54%; 40 to 45 mm, 65%; 45 to 50 mm, 72%; 50 to 55 mm, 76%). Towards the end of the pelagic juvenile stage a pale translucent layer covers the basal region of the pectoral fin and gives the black zone the appearance of a band.

Distribution.—An extensive discussion of the distribution and abundance of larvae, juveniles, and adults of *S. altivelis* is given in Moser (1974).

***Sebastolobus alascanus* Bean, Figure 26**

Literature.—Larvae, pelagic juveniles, and early demersal juveniles are described in Moser (1974).

Distinguishing features.—Larvae of *Sebastolobus* smaller than 10 mm are not separable to species. Distinguishing features of *Sebastolobus* larvae up to this size are given in the generic account and in the section describing *S. altivelis. Sebastolobus alascanus* larvae longer than 10 mm differ from those of *S. altivelis* in being less robust and in having shorter pectoral fins with a narrower base and fewer pectoral rays (Tables 29, 30). These characters carry through into the pelagic juveniles of the two species. The descriptive details for larvae and pelagic juveniles of both species are given in the section on *S. altivelis*.

In transforming species of *S. alascanus*, the first head pigment to appear is a melanistic blotch on the posterior region of the opercle. This gradually spreads anteriorally onto the cheek and in late-stage pelagic juveniles the entire head is speckled with melanophores. A blotch begins to form over each side of the gut in larvae as small as 15 mm. These enlarge dorsad onto the spinous dorsal fin and posteriad as an irregular mottled sheath that contrasts markedly with the solidly pigmented sheath of *S. altivelis* juveniles. In the largest pelagic juveniles the mottling on the dorsal fin and trunk extends posteriad to a vertical from the vent. When the juveniles become benthic the mottling spreads onto the remainder of the body and median fins. Melanophores appear on the bases of the pectoral fins in specimens of the 14- to 20-mm size range. A faint band of melanophores appears on the rays in some specimens of this size range but never becomes highly developed and covers only the basal one-third of the fin in the largest pelagic juveniles.

Distribution.—An extensive discussion of the distribution and abundance of *S. alascanus* larvae, juveniles, and adults is given in Moser (1974).

***Trachyscorpia* Ginsburg**

Literature.—None.

Distinguishing features.—**No larvae are known and the genus is known in the eastern Pacific from one adult**

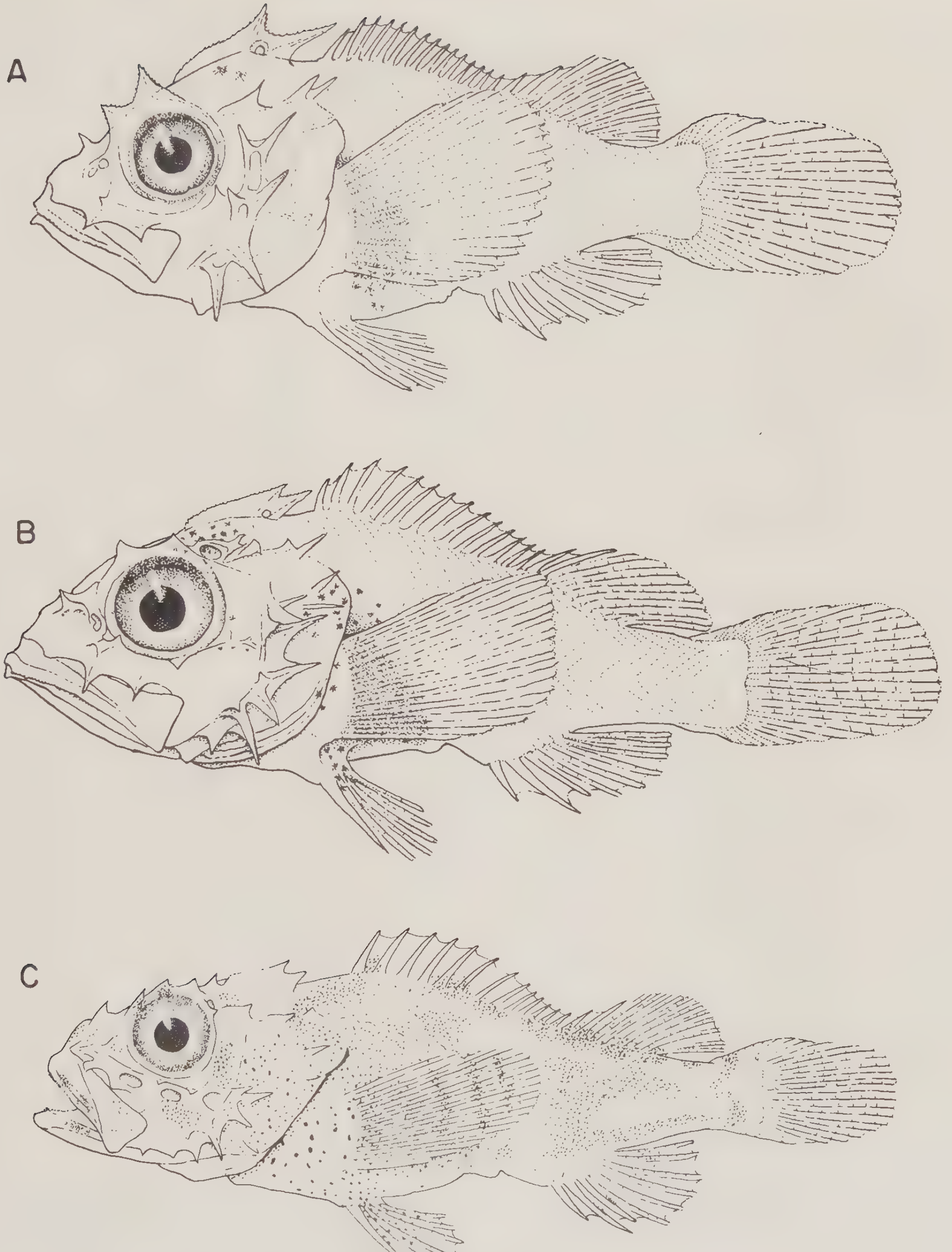

Figure 26.—Developmental series of *Sebastolobus alascanus*. A. 10.3-mm larva; B. 16.0-mm transforming specimen; C. 25.3-mm pelagic juvenile.

Table 29. Measurements (mm) of larvae and juveniles of *Sebastolobus alascanus*.

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-dorsal fin	Snout anal fin
10.3	6.2	4.2	1.5	1.2	4.0	3.2	1.6	1.9	4.3	6.8
11.2	7.4	5.0	1.8	1.3	4.1	3.2	1.7	2.1	5.0	7.7
11.7	7.2	5.0	-	1.3	3.9	3.1	1.8	2.1	5.1	7.7
12.5	7.7	4.7	1.7	1.5	4.5	3.6	1.8	2.4	5.4	8.3
13.2	7.3	5.0	1.6	1.8	4.6	3.9	1.9	2.7	5.8	8.2
14.0	8.1	5.7	1.8	2.1	4.9	4.1	1.9	2.5	6.2	8.8
14.4	8.4	5.6	1.4	1.8	5.2	4.2	2.1	2.6	5.7	9.1
15.2	9.2	6.2	1.8	2.0	5.2	4.4	2.1	2.9	6.3	10.0
16.0	9.3	6.2	2.0	2.0	5.2	4.8	2.2	2.9	7.1	10.0
16.4	9.8	6.7	1.8	2.5	5.7	4.7	2.3	3.2	7.1	10.5
16.9	10.0	6.8	1.9	2.3	5.9	4.8	2.4	3.1	7.3	10.8
17.6	10.6	6.7	2.1	2.2	6.1	4.9	2.3	3.5	7.1	11.3
18.6	12.7	-	-	2.8	6.8	5.4	2.8	3.8	8.5	13.2
19.8	12.0	7.7	2.0	2.8	7.1	5.9	2.9	4.0	8.3	13.0
20.0	12.0	8.1	2.2	2.9	7.1	5.4	2.8	4.2	8.4	13.0
20.3	12.8	8.2	1.8	3.1	7.2	6.2	7.8	4.0	8.1	13.5
21.0	13.5	8.6	1.9	3.1	7.5	6.5	3.0	4.6	8.1	14.4
21.4	12.8	8.3	2.4	2.9	7.1	6.2	2.8	3.8	8.6	14.4
21.9	12.8	8.5	2.1	3.1	7.1	6.2	2.8	4.2	8.8	14.9
22.3	14.2	9.6′	-	2.8	7.9	6.5	3.2	4.4	9.1	15.4
22.9	14.4	9.8	2.6	3.2	7.5	6.7	3.1	4.6	9.3	15.5
23.2	14.7	9.5	2.5	2.9	7.9	7.2	3.0	5.0	9.6	16.0
23.4	14.9	9.0	2.2	3.3	8.0	7.1	3.2	5.0	9.3	16.4
24.0	14.4	9.8	2.2	3.2	8.0	6.8	3.3	5.0	9.8	15.9
24.3	15.5	10.0	2.8	3.2	8.6	7.3	3.3	5.0	9.8	16.9
25.1	15.9	10.0	3.0	3.3	8.4	7.0	3.4	5.0	10.1	17.2
25.5	16.0	10.1	2.8	3.5	8.8	8.2	3.7	5.5	10.1	17.6
26.4	17.9	10.6	3.2	3.5	9.0	8.0	3.7	5.7	11.3	19.1
27.2	17.9	11.2	3.0	-	8.3	8.1	3.3	5.4	10.8	19.3
*22.5	13.0	8.7	2.1	3.2	7.2	6.3	2.9	4.6	9.6	14.7
*25.3	16.9	10.3	3.5	3.2	8.1	6.8	3.3	5.0	11.2	18.9
*37.8	22.0	12.7	2.9	5.0	10.1	9.6	4.2	8.2	13.5	24.3
*39.0	24.0	14.1	4.0	5.1	9.9	9.8	4.0	8.8	15.0	26.7
*40.8	25.1	14.8	3.8	5.3	10.0	9.7	3.8	8.8	15.3	27.3
*42.3	27.7	15.4	4.3	5.8	10.1	10.0	4.2	9.0	16.3	29.6
*43.6	26.3	15.4	4.1	5.8	9.5	10.6	4.4	9.4	16.1	29.5
*44.7	26.2	15.9	4.3	5.8	11.2	10.5	4.8	8.1	16.9	29.7
*46.2	28.1	16.2	4.4	6.4	10.8	10.8	4.7	9.9	16.7	31.2
*48.8	29.1	16.8	4.7	6.5	11.4	11.4	4.7	10.5	18.0	32.9
*50.3	29.4	17.4	4.8	7.0	12.4	12.2	5.0	10.6	18.0	33.0
*51.0	30.6	17.5	5.0	6.8	11.8	11.5	5.2	10.5	17.5	33.6
*59.2	36.6	20.6	5.4	8.4	13.0	13.5	5.6	12.1	20.8	40.0
*60.0	36.8	21.6	5.7	9.0	14.3	14.3	5.9	13.0	21.5	39.7

* Benthic juvenile.

specimen reported as *Trachyscorpia* sp. (Chirichigno 1974). The specimen was collected off Peru at lat. 13°57.2′S and long. 76°42′W in 580 to 600 m. Eschmeyer (pers. commun.), who has examined the specimen, finds no obvious difference between it and *T. cristulata* from the Atlantic. If Eschmeyer (1969) is correct in the placement of *Trachyscorpia* near *Sebastolobus* in the subfamily Sebastolobinae, its larvae can be expected to share some of the features of *Sebastolobus* larvae.

Scorpaenodes Bleeker

Literature.—The literature contains no descriptions or illustrations of the developmental stages of *Scorpaenodes*.

Distinguishing features.—*Scorpaenodes* larvae differ from all other known Scorpaenidae except *Sebastolobus*, in having prominent crestlike parietal ridges that terminate in double spines, the posterior (nuchal) spines being more prominent than the anterior (parietal) spine; in larvae of other known scorpaenid genera, if two spines are present on the parietal ridge, the second is smaller and subjacent to the first. *Scorpaenodes* differs markedly from *Sebastolobus* in melanophore pattern and in degree of development at comparable sizes. Newly hatched *Scorpaenodes* larvae have a series of about a

Table 30. **Meristics from cleared and stained larvae and juveniles of *Sebastolobus alascanus*.**

Length (mm)	Primary caudal fin rays		Secondary caudal fin rays		Branchiostegal rays		Pectoral fin rays		Hypural elements		Gill rakers (right arch)		Anal fin rays	Dorsal fin rays	Pelvic fin rays		Vertebrae
	Superior	Inferior	Superior	Inferior	Left	Right	Left	Right	Superior	Inferior	Upper limb	Lower limb			Left	Right	
7.5	8	7	3	4	7	7	21	21	2	2	3	9	III-5	XVI-8	I-5	I-5	30
11.0	8	7	3	5	7	7	22	22	1	2	4	9	III-5	XVI-9	I-5	I-5	30
11.7	8	7	6	6	7	7	22	22	2	2	4	10	III-5	XVI-8	I-5	I-5	30
12.5	8	7	7	8	7	7	21	21	2	2	5	12	III-5	XVI-10	I-5	I-5	30
13.2	8	7	8	7	7	7	21	22	2	2	5	12	III-5	XVI-9	I-5	I-5	30
14.4	8	7	9	9	7	7	22	22	2	2	5	13	III-5	XVI-9	I-5	I-5	30
15.2	8	7	8	8	7	7	22	22	2	2	5	12	III-5	XVI-9	I-5	I-5	30
16.4	8	7	9	9	7	7	21	21	2	2	7	13	III-5	XVII-9	I-5	I-5	30
17.6	8	7	9	9	7	7	21	21	2	2	6	13	III-5	XVI-9	I-5	I-5	30
18.6	8	7	9	9	7	7	22	22	2	2	6	13	III-5	XVI-9	I-5	I-5	30
19.8	8	7	8	8	7	7	22	22	2	2	6	13	III-5	XVI-9	I-5	I-5	31
20.3	8	7	9	8	7	7	22	22	2	2	5	13	III-5	XVI-9	I-5	I-5	30
21.4	8	7	8	8	7	7	22	22	2	2	6	13	III-5	XVI-9	I-5	I-5	30
22.3	8	7	8	8	7	7	22	22	2	2	6	12	III-5	XVI-9	I-5	I-5	30
24.3	8	7	9	8	7	7	21	21	2	2	7	14	III-4	XVI-9	I-5	I-5	30
25.5	8	7	9	9	7	7	22	22	2	2	6	14	III-5	XV-10	I-5	I-5	30
26.4	8	7	9	9	7	7	21	21	2	2	7	12	III-5	XV-9	I-5	I-5	30
27.2	8	7	10	10	7	7	21	21	2	2	7	13	III-5	XVI-10	I-5	I-5	30

dozen melanophores along the ventral midline of the tail. These soon become embedded and are not visible in larvae larger than 4.0 mm. Newly hatched *Sebastolobus* larvae lack this series of melanophores, but have two large melanistic blotches about midway along the tail. *Scorpaenodes* larvae lack the melanistic shield that covers the dorsolateral surfaces of the gut in larvae of *Sebastolobus, Scorpaena,* and *Sebastes*. In place of this, small *Scorpaenodes* larvae have a deeply embedded blotch just dorsal to the axilla. This later enlarges to cover the dorsal surface of the gas bladder. Head spine and caudal fin formation occur at smaller sizes in *Scorpaenodes* compared with *Sebastolobus*. In *Scorpaenodes*, numerous head spines are present in larvae less than 3.0 mm long, while *Sebastolobus* of that size still have their yolk and do not obtain a comparative degree of spine development until they are twice that size. In *Scorpaenodes*, notochord flexion occurs within the size range of 4.0 to 5.5 mm whereas in *Sebastolobus* it occurs in the range of 6.0 to 7.5 mm.

Scorpaenodes xyris (Jordan and Gilbert), Figures 27-29

Literature.—There are no previous descriptions or illustrations of *Scorpaenodes* larvae.

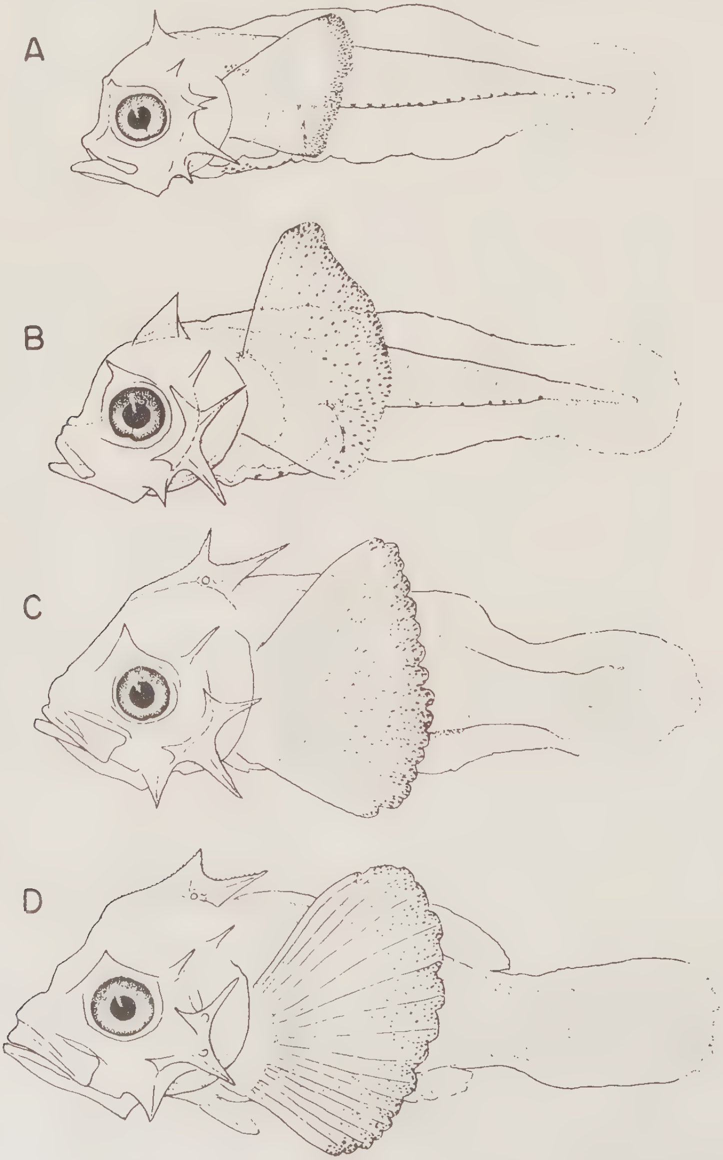

Figure 27.—Larvae of *Scorpaenodes xyris*. A. 2.7 mm; B. 3.2 mm; C. 4.0 mm; D. 4.8 mm.

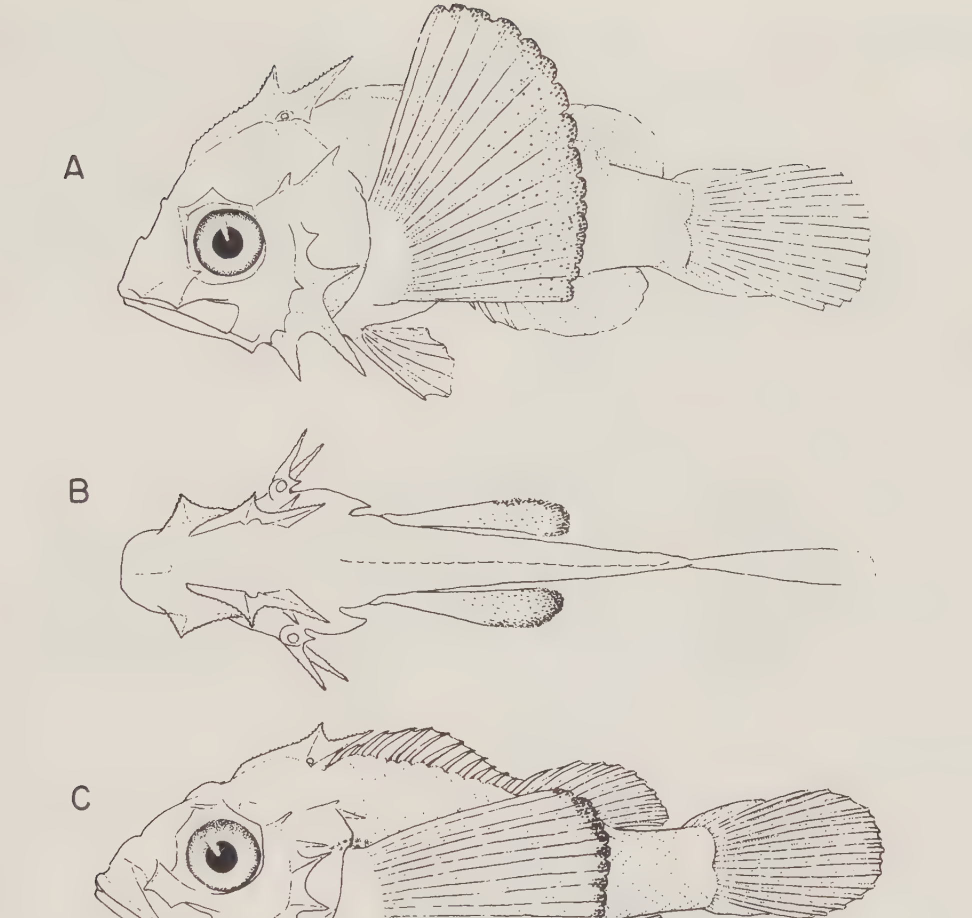

Figure 28.—Larvae of *Scorpaenodes xyris*. A. 6.2 mm; B. 6.2 mm, dorsal view; C. 9.2 mm; D. 13.0 mm.

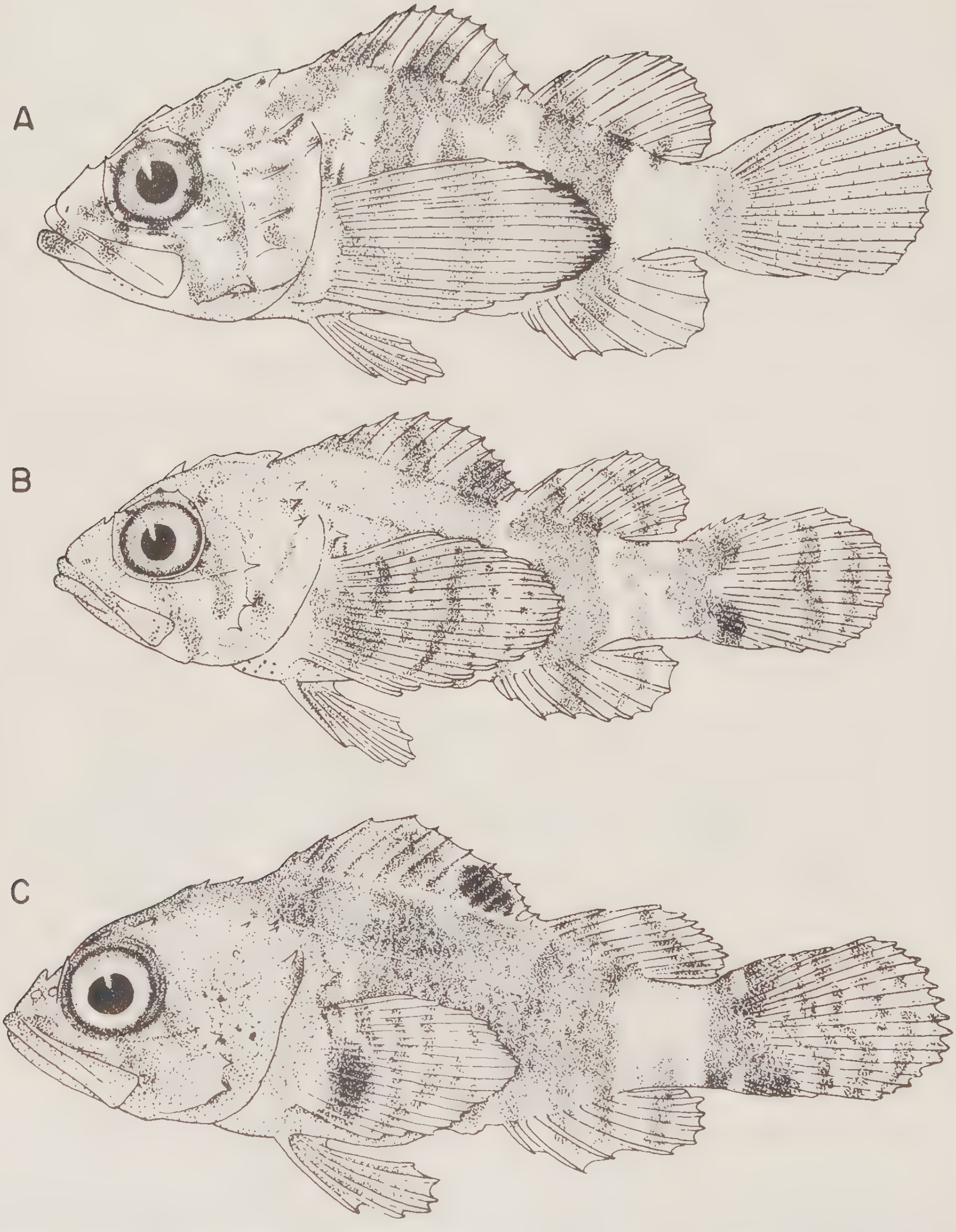

Figure 29.—Developmental series of *Scorpaenodes xyris*. A. 12.5-mm transforming specimen; B. 11.8-mm benthic juvenile; C. 12.7-mm benthic juvenile.

Distinguishing features.—A single species of *Scorpaenodes*, *S. xyris*, is known from the eastern Pacific. Comparison of *S. xyris* larvae with those of congeners is not possible since we have only *S. xyris* larvae in our collections.

The smallest larvae of *S. xyris* in our collections are 1.8 mm in length. These specimens have already exhausted their yolk supply, so it is likely that newly hatched larvae of *S. xyris* are slightly smaller than 1.8 mm. Larvae reach a maximum length of 14.0 mm and transformation into benthic juveniles occurs within a size range of 11.0 to 14.0 mm.

Scorpaenodes xyris larvae are deep-bodied; body depth increases gradually during the larval period. It averages 28% of body length before notochord flexion, 33% during flexion, and 39% after the completion of flexion (Table 31). In the slightly more elongate transforming specimens and newly transformed juveniles, body depth is 36% of body length.

Table 31. Measurements (mm) of larvae of Scorpaenodes xyris. (Specimens between dashed lines are undergoing notochord flexion.)

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-anal fin distance
2.7	1.2	0.80	0.20	0.28	0.78	0.27	0.21	-	-
3.2	1.5	1.0	0.25	0.32	0.84	0.84	0.54	-	-
3.8	1.8	1.1	0.37	0.32	1.0	0.97	0.67	-	-
3.9	1.8	1.2	0.48	0.37	1.2	1.1	0.68	-	-
4.0	1.9	1.4	0.49	0.35	1.2	1.2	0.76	-	-
4.2	2.0	1.2	0.50	0.38	1.2	1.2	0.71	0.03	-
4.2	2.0	1.3	0.46	0.35	1.2	1.3	0.75	0.03	2.4
4.3	2.0	1.3	0.50	0.39	1.2	1.5	0.83	0.12	2.4
4.4	2.3	1.5	0.48	0.35	1.4	1.4	0.85	0.15	2.8
4.6	2.4	1.5	0.55	0.51	1.6	1.6	0.83	0.21	2.5
4.9	2.8	2.0	0.72	0.54	1.8	1.8	0.91	0.40	2.9
5.2	2.8	1.9	0.68	0.60	1.9	1.9	1.0	0.50	2.5
5.4	3.2	2.1	0.76	0.55	2.0	2.2	1.1	0.70	3.2
5.6	3.2	2.0	0.70	0.58	2.1	2.1	1.2	0.60	3.2
5.8	3.6	2.4	0.75	0.65	2.3	2.2	1.1	0.80	3.6
6.2	3.6	2.3	0.78	0.70	2.4	2.3	1.2	1.0	3.7
6.5	3.8	2.4	0.83	0.75	2.4	2.8	1.2	1.4	3.9
6.8	4.2	2.6	0.92	0.77	2.7	2.5	1.2	1.1	4.2
7.0	4.3	2.8	0.90	0.88	2.7	2.9	1.3	1.2	4.5
7.2	4.5	2.8	0.80	0.82	2.9	2.8	1.3	1.2	4.7
7.5	4.2	2.5	0.84	0.88	3.0	2.8	1.4	1.3	4.3
7.7	4.8	3.1	1.1	0.90	2.8	2.8	1.5	1.4	4.8
7.9	4.4	3.1	1.0	0.86	2.8	2.9	1.4	1.2	4.8
8.2	5.1	2.9	0.92	0.93	3.2	3.3	1.5	1.8	5.3
8.6	5.2	3.2	1.0	1.0	3.3	3.2	1.4	1.7	5.3
9.0	5.4	3.3	1.0	1.0	3.5	3.9	1.7	1.7	5.5
9.2	5.0	3.5	1.2	1.0	3.4	3.6	1.6	1.5	5.3
9.5	6.3	3.9	1.2	1.2	3.8	3.5	1.6	1.8	6.4
9.8	5.8	3.6	1.1	1.1	3.6	4.3	1.7	1.7	6.1
10.0	6.1	3.6	1.1	1.2	4.1	4.5	1.8	1.9	6.2
10.3	6.8	4.1	1.2	1.3	4.1	3.8	1.8	1.7	6.8
10.6	6.9	4.1	1.2	1.3	3.8	3.8	1.8	1.7	7.0
11.0	6.4	4.2	1.3	1.4	4.2	4.2	1.8	2.0	6.5
11.7	7.7	4.6	1.3	1.4	4.3	4.2	2.2	2.4	7.9
12.2	7.3	4.3	1.4	1.5	5.0	5.2	2.2	2.6	7.8
13.0	8.6	4.3	1.2	1.6	5.2	5.2	2.1	2.2	8.8
*11.0	6.8	3.9	1.0	1.3	3.8	3.9	1.9	2.1	7.3
*11.8	7.6	4.6	1.2	1.4	4.2	4.1	2.0	2.3	8.1
*12.5	8.1	4.8	1.2	1.7	4.6	4.9	2.2	2.4	8.7
**12.5	8.2	4.8	1.1	1.8	4.4	4.2	2.1	2.7	8.8

*Transforming specimen.

**Benthic juvenile.

The gut is compact in small larvae of *S. xyris*. Snout-anus distance undergoes a relative increase throughout the larval period. It averages 46% of body length prior to notochord flexion, 52% during flexion, 61% in postflexion larvae, and 64% in transforming specimens.

The large spiny head is a prominent feature of *S. xyris* larvae. Head length increases from a mean of 30% of body length in preflexion larvae to 34% in larvae undergoing notochord flexion, to 38% in postflexion larvae and transforming specimens. The eyes are relatively small; eye diameter averages 30% of the head length for the entire larval period with no obvious trend of relative increase or decrease. The snout length is relatively short in newly hatched larvae (25% of head length), increases to a relative maximum length during notochord flexion (average of 36% of head length), and then gradually decreases during the remainder of the larval period to 25% of head length.

The smallest larvae (1.8 mm) in our collection have pectoral fins with the base and blade well differentiated. The fins enlarge rapidly and are prominent fan-shaped structures in larvae larger than 3.0 mm. Fin length averages 22% of body length prior to notochord flexion, 34% during flexion, and 39% during the remainder of the larval period. They shorten during transformation (average of 36%) and are about 35% in newly transformed juveniles. The base of the pectoral fin is wide as in other scorpaenine genera. It averages 18% of the body length for the entire larval period. Ossification of the rays begins in 4-mm larvae (Table 32). The full complement of 16 to 19 rays is present in larvae longer than 4.7 mm.

Table 32. Meristics from cleared and stained larvae of Scorpaenodes xyris.

Length (Mm)	Principal caudal fin rays		Procurrent caudal fin rays		Branchiostegal rays		Pectoral fin rays		Hypural elements		Gill rakers (right arch)		Anal fin rays	Dorsal fin rays	Pelvic fin rays		Vertebrae
	superior	inferior	superior	inferior	left	right	left	right	superior	inferior	upper limb	lower limb			left	right	
4.2	-	-	-	-	4	4	-	-	-	-	-	-	-	-	-	-	-
4.6	8	7	-	-	7	7	17	17	-	-	0	5	-	-	I-2	I-2	18
5.2	8	7	2	2	7	7	16	16	2	1	1	6	III-5	XIII-7	I-5	I-5	24
5.8	8	7	3	3	7	7	17	17	2	2	2	7	III-5	XIII-9	I-5	I-5	24
6.0	8	7	4	4	7	7	17	17	2	2	2	7	III-5	XIII-9	I-5	I-5	25
6.7	8	7	4	4	7	7	17	16	2	2	3	7	III-5	XIII-9	I-5	I-5	24
7.2	8	7	4	4	7	7	17	17	2	2	3	7	III-5	XIII-9	I-5	I-5	24
7.9	8	7	4	4	7	7	18	18	2	2	2	8	III-5	XIII-9	I-5	I-5	24
8.2	8	7	4	4	7	7	17	17	3	2	3	9	III-5	XIII-9	I-5	I-5	24
9.5	8	7	4	4	7	7	17	18	3	2	4	10	III-5	XIII-9	I-5	I-5	24
10.3	8	7	4	4	7	7	17	17	3	2	3	10	III-5	XIII-9	I-5	I-5	24
11.7	8	7	4	4	7	7	19	19	3	2	3	9	III-5	XIII-9	I-5	I-5	24

The anlage of the caudal fin is present in 2-mm larvae. The hypurals begin to ossify in 5-mm larvae and the full complements of 3 superior and 2 inferior elements are ossified in 8-mm larvae. The principal caudal rays begin to ossify in 4-mm larvae and the full complement of 8 superior and 7 inferior rays is present in a 4.6-mm larva. The procurrent caudal rays begin to ossify in 5-mm larvae and the full complements of 4 superior and 4 inferior rays are present in 6-mm larvae.

The pelvic fin appears in 4-mm larvae and increases in length to 13% of body length at the completion of notochord flexion. Fin length averages 18% of body length for the remainder of the larval period. The rays begin to ossify in 4-mm larvae, and the full complement of 1 spinous ray and 5 soft rays is present at 4.6 mm in length.

The dorsal and anal fins begin to develop simultaneously in 4-mm larvae. Ossification of the rays begins in 5-mm larvae and the full complements of XIII, 9 (10) dorsal rays and III, 5 anal rays are present before the larvae reach 6.0 mm.

Pigmentation is sparse in *S. xyris* larvae. The smallest larvae in the collection have a series of 12 to 18 melanophores along the ventral midline of the tail, from the junction of the gut to the hypural anlage. They also have a patch of melanophores along the ventral midline of the gut and several melanophores on the terminal section of the gut. Also, there is an embedded blotch just dorsal to the axilla and the distal region of each pectoral fin is covered with fine melanophores.

As development proceeds some of this original pigment pattern is lost. The series on the ventral midline of the tail is lost before the larvae reach 4.0 mm. The melanophores at the ventral midline of the gut are lost in larvae between 4.0 and 4.5 mm. The patch median to the axillary region enlarges to form a shield over the gas bladder and is visible throughout the larval period.

Just before transformation, a group of melanophores appears on the opercle and preopercle. Transforming specimens from bottom collections have a striking mottled pattern on the head and body. In some, the distal margin of the pectoral fin is still melanistic.

Distribution.—*Scorpaenodes xyris* is a coastal warm-water species. Adults have a latitudinal range from Peru northward to San Clemente Island, Calif., and occur off islands such as Guadalupe and the Galapagos (Miller and Lea 1972). CalCOFI surveys show that the larvae occur throughout the lower two-thirds of the Gulf of California. On the outer coast, *S. xyris* larvae were found only as far north as line 117 (about lat. 28°N) off Punta Eugenia. The planktonic collections of the EASTROPAC expedition show that *S. xyris* larvae occur from lat. 20°N to lat. 20°S along a coastal band (Fig. 30). Larvae occurred in small numbers in both CalCOFI and the eastern tropical Pacific hauls. The largest number taken on any haul was seven, and three-fourths of the positive hauls had a single larva of *S. xyris*.

Larvae were taken on all CalCOFI cruises in the Gulf of California (Fig. 30). More larvae were taken in June than in the other months (February, April, December), thus suggesting a summer spawning peak in this region. On EASTROPAC expeditions, the number of occurrences was about equal on the winter cruises (February-April) and the summer cruises (July-September).

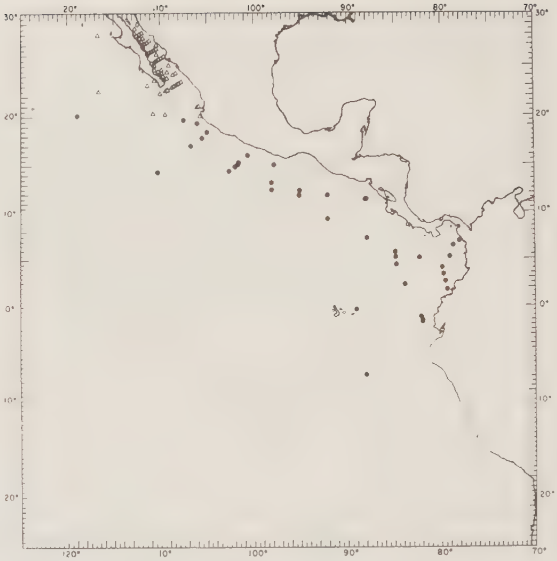

Figure 30.—Stations at which larvae of *Scorpaenodes xyris* were taken on CalCOFI cruises (triangles) during 1956 and 1957 and EASTROPAC expeditions (dots) during 1967 and 1968.

Scorpaena Linnaeus

Literature.—The early stages of two North Atlantic-Mediterranean species of *Scorpaena, S. porcus* and *S. scrofa*, were described by Raffaelle (1888) and Fage (1918). More thorough descriptions of the egg, larval, and juvenile stages of these two species and of the eggs and larvae of *S. notatus* were given by Sparta (1941, 1942, 1956). The latter paper includes a color plate. The early developmental stages of the sculpin, *Scorpaena guttata*, of California and Baja California were described from specimens cultured in aquaria (Barnhart 1932; David 1939; Orton 1955). These authors described the egg masses, developing eggs, and larvae up to the stage of yolk exhaustion (about 3.0 mm body length).

Distinguishing features.—*Scorpaena* larvae are easily distinguished from *Sebastes* and *Sebastolobus* by myomere count, *Scorpaena* having 24, *Sebastes* having 26 or more, and *Sebastolobus* having 28 or more. *Scorpaena* differs further from *Sebastolobus* in having a row of melanophores along the ventral midline of the tail, as opposed to a single dorsal and ventral blotch, and in having nonbifurcate parietal ridges. This latter character also separates *Scorpaena* from *Scorpaenodes*. *Scorpaena* larvae develop a moderately long pair of parietal spines that reach their greatest relative length at about the completion of caudal fin formation. A small nuchal spine forms subjacent to each parietal spine. *Scorpaena* may be separated from *Pontinus* on the basis of gut pigmentation. *Scorpaena* larvae develop a melanistic shield over the dorsolateral surface of the gut, whereas *Pontinus* larvae have a deeply embedded blotch above the axillary region which, as in *Scorpaenodes*, enlarges to cover the dorsal surface of the gas bladder. This character is particularly useful in separating small larvae of *Scorpaena*, *Pontinus*, and *Scorpaenodes* that have not yet formed head spines. Another melanistic character useful in separating *Scorpaena* larvae from those of *Scorpaenodes* and *Pontinus* is the presence of a ventral midline blotch just anterior to the juncture of the cleithra in *Scorpaena*. This is absent in the other five genera.

Scorpaena larvae have highly characteristic pectoral fins. They are moderate in length, as opposed to the extremely elongate fins of *Scorpaenodes*, and are fan-shaped in contrast to the aliform pectorals of *Pontinus*. Pigmentation varies among the species of *Scorpaena*, but the pectorals are usually heavily pigmented.

According to a recent revision, there are nine species of *Scorpaena* in the eastern Pacific (Greenfield 1974). *Scorpaena* larvae usually occur nearshore, thus are not common constituents of our plankton hauls. Our collections contain sufficient numbers of larvae for the following descriptions of *S. guttata* and another form which we designate as Type A.

Scorpaena guttata Girard, Figure 31

Literature.—The three publications on the early developmental stages of *S. guttata* listed in the preceding section describe stages up to 3.0 mm. Later larval stages of *S. guttata* have not been previously described.

Distinguishing features.—The early stages of *Scorpaena guttata* have been studied in detail (Barnhart 1932; David 1939; Orton 1955) and the following account is a summary of these studies. The egg masses are spawned at about midnight and float to the surface. They are bilobed gelatinous structures, each lobe measuring 16 to 26 cm in length. The matrix is about 2-mm thick and within it the eggs are evenly spaced in a single layer. The slightly elliptical eggs measure about 1.2 mm at the long axis. The yolk mass is colorless and contains no oil globule. The chorion is colorless, transparent, and unsculptured. There is no apparent perivitelline space. The eggs hatch when freed from the matrix at an average time of 3 days after fertilization in southern California waters. The newly hatched young are 1.9 to 2.0 mm long, have a large elliptical yolk sac, and have a voluminous dorsal finfold that is inflated in appearance. The pectoral fin buds are small and inconspicuous. A patch of dendritic melanophores covers the dorsal aspect of the gut and similar melanophores are also below the gut.

At about 4 days after fertilization, the larvae are 2.5 to 2.7 mm long, have 22 to 24 myomeres, and have a row of melanophores along the ventral midline of the tail. At about 5 days after fertilization, the yolk is half utilized, and at about 6 days the mouth is formed. At 7 to 8 days the yolk is depleted, the jaws are functional, and the pectorals are fan-shaped and have one to several rows of melanophores along their distal margins. The previously undescribed later larval stages of *S. guttata* are delineated below.

Early-stage larvae of *S. guttata* are deep-bodied, become comparatively more slender during notochord flexion, and thereafter become increasingly deep-bodied. Body depth averages 36% of body length prior to notochord flexion, 30% during flexion, and 40% following flexion (Table 33).

The compact gut increases gradually in relative length during the larval period. Snout-anus length averages 49% of body length prior to notochord flexion, 51% during flexion, and 60% following flexion.

At the completion of yolk utilization the head of *S. guttata* larvae is moderately large and increases in relative size during later larval development. Head length averages 30% of body length in preflexion larvae, 34% during flexion, and 38% following flexion. The eyes are moderately small; eye diameter averages 32% of the head length throughout the larval period with no obvious trend of relative increase or decrease. Snout length increases from an average of 31% of the head length in preflexion larvae to 33% in larvae undergoing flexion, then decreases gradually to 28% in our largest larva.

The pectoral fins are small and poorly differentiated in 2.0-mm larvae but growth and differentiation is rapid and, when the larvae have reached 3.0 mm, the fins have a well-differentiated base, a deep fan-shaped blade, and have doubled in length to 15% of the body length. Fin length increases to an average of 21% of the body length at notochord flexion. Following notochord flexion, fin length averages 22% of body length up to about 10 mm, and then there is a considerable jump in relative fin length to 29% in our largest larva (12.8 mm). The depth of the fin base is slightly smaller than in other scorpaenine genera. It averages 15% of the body length over the entire larval period. Fin rays begin to ossify in larvae about 4.0 mm long and the full complement of 17 to 19 rays is present in 5-mm larvae.

The hypural anlagen of the caudal fin are apparent in larvae as small as 2.5 mm. They begin to ossify in 5-mm larvae and in the largest stained specimen (6.5 mm) the large superior and inferior elements are well ossified. The

Table 33. Measurements (mm) of larvae of Scorpaena guttata. (Specimens between dashed lines are undergoing notochord flexion.)

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-anal fin distance
0	1	0.38	0.11	0.18	0.90	0.14	0.15		-
9	1.4	0.95	0.27	0.26	1.1	0.45	0.37		-
2	1.[illegible]	1.0	0.[illegible]	0.32	1.1	0.57	0.50		-
9	1.7	1.2	0.35	0.35	1.3	0.60	0.62	-	-
[illegible]	2.1	1.2	0.44	0.45	1.2	0.93	0.69	0.08	-
5	2.2	1.6	0.56	0.45	1.3	1.0	0.75	0.10	2.6
4.8	2.4	1.7	0.52	0.52	1.4	1.0	0.78	0.12	2.7
4	2.7	1.7	0.60	0.55	1.5	1.0	0.83	0.11	3.1
7	3.2	2.0	0.67	0.67	1.8	1.2	0.94	0.32	3.4
8	3.2	2.0	0.68	0.68	2.1	1.2	1.0	0.55	3.3
0	3.5	2.2	0.76	0.72	2.2	1.4	1.0	0.60	3.6
5	3.7	2.3	0.80	0.78	2.4	1.5	1.1	0.73	3.7
0	5.1	3.[illegible]	[illegible]	1.1	3.5	1.8	1.3	1.6	5.2
2	5.5	3.8	1.2	1.0	3.8	2.0	1.4	1.6	5.6
8	6.0	3.8	1	1.1	3.9	1.8	1.5	1.7	6.1
8	7.9	5.0	1.4	1.8	5.4	3.7	1.8	2.6	8.2

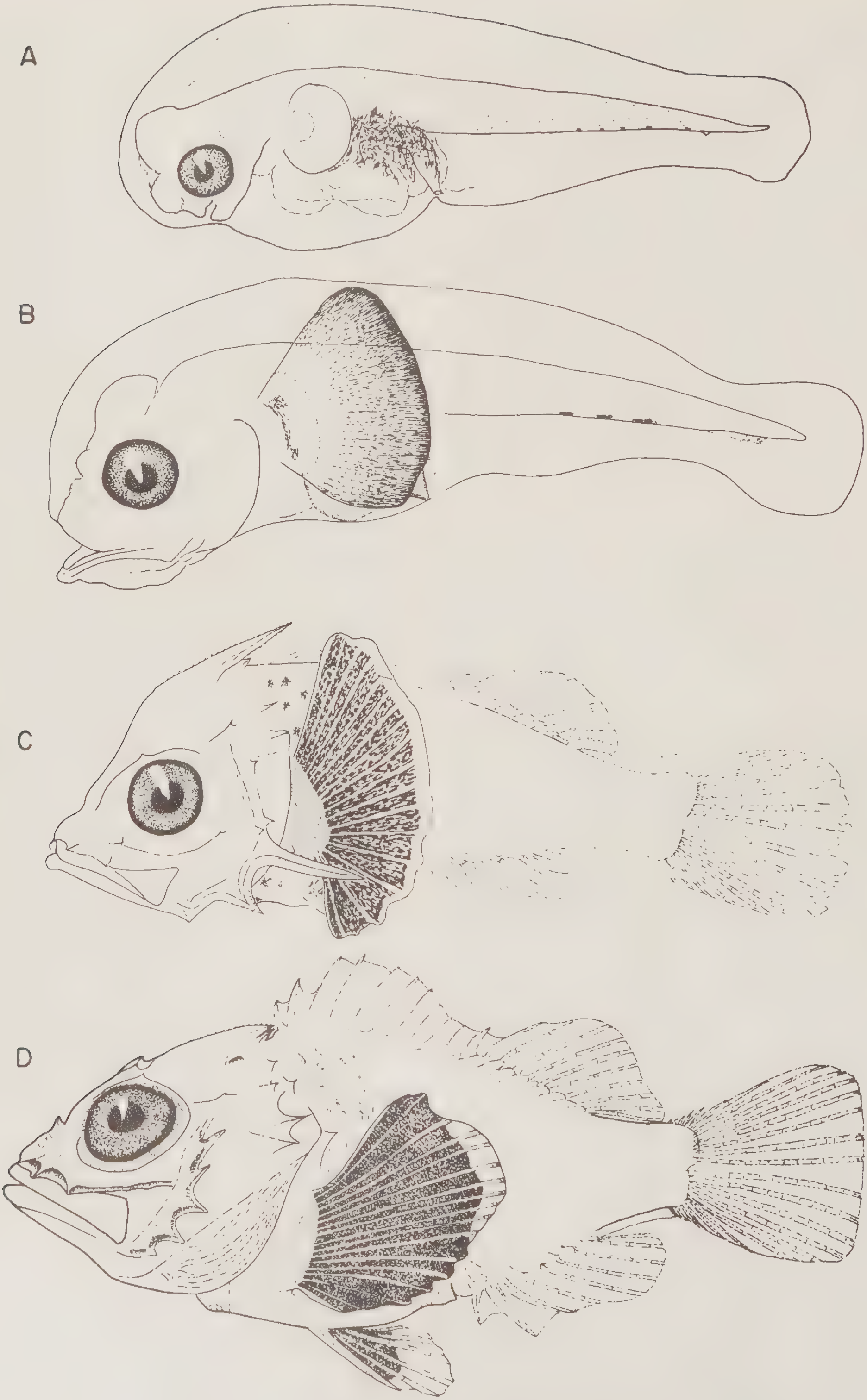

Figure 31.—Larvae of *Scorpaena guttata*. A. 2.1 mm; B. 3.1 mm; C. 6.2 mm; D. 12.8 mm.

full complement of 8 + 7 principal caudal rays is undergoing initial ossification in a larva 5.2 mm long. Secondary caudal rays begin ossifying in 5-mm larvae. In the largest stained specimen (6.5 mm) there are 4 superior and 4 inferior secondary elements ossifying.

The pelvic fins appear when the larvae are about 4.0 mm long and increase in relative length to 10% of the body length at the completion of notochord flexion. There is a gradual elongation of the fin during later larval stages to a maximum of 20% of the body length in our largest larva. Pelvic fin rays begin ossifying in 5-mm larvae and the full complement of 1 spinous ray and 5 soft rays is ossifying before the larvae reach 6.0 mm.

The dorsal and anal fins begin to form simultaneously in larvae about 4.5 mm long. Ossification begins in 5-mm larvae and the full complements of III, 5 or 6 anal rays and XII, 8 to 10 dorsal rays is present in 6-mm larvae.

Larvae of *S. guttata* are characteristically pigmented. Pigmentation of larvae less than 3.0 mm long has been described by other investigators and is summarized above. Notable changes occur in the initial pigment pattern in larvae larger than 3.0 mm. Melanophores first appear on the posterior margin of the pectoral fin in early larvae and when the larvae are 3.2 mm long, the distal half of the fin is covered. At 4.0-mm length, the entire fin is covered with melanophores as is the medial surface of the fin base. As the rays develop, the pigment becomes restricted to the membrane between the rays and becomes strikingly heavy. In 6-mm larvae the distal margin of each fin begins to lose pigment and this clear zone widens to about 20% of the length of the fin in the largest larva. Gut pigment was originally on the dorsolateral surface of the gut, but spreads ventrally to cover all surfaces of the gut when the larvae reach 4.0 mm. There is a gradual reduction in the number of pigment spots in the ventral tail series. In larvae about 3.0 mm long the number of melanophores in this series ranges from 2 to 7 with a mean of 4.15 ± 1.62 SD for 50 larvae. In larvae between 3.0 and 8.0 mm there is a general decline in this number but the average number for the whole size range is 2.64 ± 1.12 for 11 larvae. Larvae longer than 9.0 mm had no ventral tail melanophores.

When the larvae reach 4.0 mm, a small blotch of pigment develops just anterior to the cleithral symphysis. This remains throughout the larval period and is augmented by several more melanophores in larvae larger than 9.0 mm. Melanophores develop on the head region in larvae of about 4.5 mm in length. A single melanophore is embedded at the nape and persists through the remainder of the larval period. It is augmented by several more melanophores in larvae 8.0 mm and longer. A pair of melanophores appears above the optic lobes of the brain in 4.5-mm larvae and to these are added other melanophores until the optic lobes are covered in larvae larger than 9.0 mm. A pair of melanophores forms above the olfactory lobes in larvae about 6.0 mm long and persists throughout the remainder of the larval period. Several melanophores form around the base of the pelvic fins in larvae about 6.0 mm long, but the fins themselves remain unpigmented until late in the larval period. Melanophores begin to form in the epaxial myosepta above the pectoral fin in some larvae as small as 6.2 mm and cover an extensive area in larvae larger than 10.0 mm. Melanophores appear on the cheek and below the eye in 9-mm larvae and become more extensive in larger larvae.

Distribution.—Adults of *S. guttata* are known from Santa Cruz, Calif., southward to Uncle Sam Bank, Baja California (about lat. 24°35′N). This species also occurs at Guadalupe Island, Baja California, and in the northern part of the Gulf of California (Miller and Lea 1972). Distribution of *S. guttata* larvae was analyzed for the 1966 and 1969 CalCOFI cruises. Larvae were taken from June to November in 1966 and from July to September in 1969. Spawning appears to peak in August, as 44% of the total occurrences and 67% of the larvae for 1966 were taken during this month (Table 34).

Table 34. Numbers of occurrences and standardized numbers of larvae of *Scorpaena guttata* taken by CalCOFI in 1966.

CalCOFI line	Latitude[1] (N)	June		July		August		September		October		November	
		Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.	Occ.	No.
97	32°17.5′	-	-	-	-	1	3	-	-	-	-	-	-
100	31°42.2′	-	-	-	-	1	3	2	6	-	-	-	-
103	31°07.0′	1	3	1	2	-	-	1	12	-	-	-	-
107	30°27.9′	-	-	-	-	2	5	2	6	-	-	-	-
110	29°52.0′	-	-	-	-	2	9	-		-	-	-	-
113	29°24.2′	-	-	1	3	1	3	3	28	-	-	-	-
117	28°58.0′	-	-	3	16	6	104	2	15	1	6	-	-
118	28°18.5′	-	-	-	-	1	3	1	9	-		-	-
119	28°19.0′			-	-	1	3	-		-	-	-	-
120	28°25.0′	-	-	4	12	4	52	-		1	3	-	-
123	27°26.2′	-	-	1	2	2	28	-	-	1	3	-	-
127	26°57.5′	-	-	4	12	1	62	-	-	-	-	-	-
130	26°33.5′	-	-	1	2	1	5	-	-	-	-	-	-
133	26°08.5′	-	-	1	3	4	29	-	-	-		-	-
137	25°36.1′	-	-	2	5	-	-	-	-	1	2	1	8

[1] Latitude of most shoreward station.

Larvae of *S. guttata* occur in the southern portion of the CalCOFI pattern, from about the Mexican border south to line 137, just north of Magdalena Bay (Table 34). The greatest concentration of positive hauls was off central Baja California in the area around Punta Eugenia (Fig. 32).

Scorpaena Type A, Figure 33

Literature.—This larval form of *Scorpaena* has not been previously described or illustrated.

Distinguishing features.—Egg masses of *Scorpaena* species other than *S. guttata* have not been reported in the eastern Pacific and yolk-sac stages of Type A larvae are not present in our collection. Type A larvae are similar morphologically to those of *S. guttata*, but are comparatively more slender prior to notochord flexion. Body depth at this stage averages 27% of body length for Type A larvae (Table 35) and 36% for *S. guttata*. Body depth for Type A larvae undergoing notochord flexion averages 29% of body length, and for postflexion stages the mean is 38%. Comparative percentages for *S. guttata* larvae are 30% and 40%.

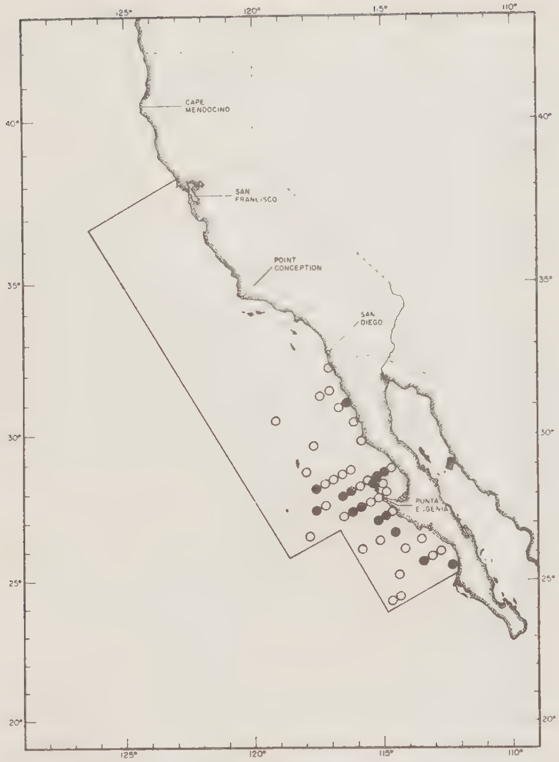

Figure 32.—Stations at which larvae of *Scorpaena guttata* were taken on CalCOFI cruises during 1966. Solid circles indicate stations where number of larvae exceeded mean (7.4) for all positive stations. Area of complete grid is outlined (see Ahlstrom 1961 for complete grid).

Table 35. Measurements (mm) of larvae of Scorpaena Type A. (Specimens between dashed lines are undergoing notochord flexion.)

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-anal fin distance
2.2	1.2	0.58	0.20	0.22	0.57	0.23	0.26	-	
2.5	1.2	0.70	0.23	0.25	0.67	0.27	0.31		-
2.8	1.4	0.73	0.21	0.22	0.66	0.28	0.40		
3.0	1.4	0.87	0.26	0.30	0.96	0.42	0.43	-	-
3.5	1.8	1.0	0.33	0.36	1.15	1.52	0.52		
3.7	1.8	1.0	0.34	0.33	0.98	0.47	0.55		
4.0	[illegible]	1.2	0.4	0.46	1.2	0.65	0.60	0.05	2.2
4.2	2.1	1.3	0.4	0.40	1.3	0.65	0.65	0.07	2.3
4.6	2.3	1.5	0.48	0.42	1.4	0.75	0.68	0.10	2.6
5.0	2.7	1.6	0.50	0.51	1.4	0.77	0.73	0.07	2.8
5.5	3.1	1.9	0.62	0.60	1.5	1.0	[illegible]	0.18	[illegible]
5.8	3.4	2.2	0.73	0.73	[illegible]	1.1	0.97	0.69	3.4
6.1	3.8	2.3	0.70	0.72	2.1	1.2	1.1	0.53	3.8
6.8	[illegible]	2.5	0.75	0.99	2.8	1.3	1.2	1.1	4.2
7.0	[illegible]	2.6	0.83	0.90	2.8	1.5	1.2	[illegible]	[illegible]
7.6	4.8	2.9	0.91	1.0	[illegible]	1.7	1.2	1.1	4.8
8.0	4.8	3.1	0.93	1.1	3.5	1.8	1.4	1.4	4.8
12.2	[illegible]	5.2	1.6	1.7	5.7	4.0	2.0	1.9	9.2

The gut is compact and increases in relative length during the larval period. Snout-anus length averages 50% of body length prior to notochord flexion, 53% during flexion, and 61% following flexion. Head size is moderate and increases relative to body length during development. Head length averages 28% up to the beginning of notochord flexion, 32% during flexion, and 38% following flexion. Snout length and eye diameter show no change relative to head size and average 32% and 33% of head length, respectively.

The fan-shaped pectoral fins are similar in size to those of *S. guttata*. They increase in relative length from an average of 12% of body length in preflexion larvae to 16% during flexion, and 21% following flexion. Depth of the fin base shows a more gradual relative increase of 14%, 15%, and 17% for the three stages. Pectoral fin rays begin to ossify in 3-mm larvae and the full complement of 19 to 20 rays is present in 4-mm larvae. The pelvic fins begin to form in 4-mm larvae and reach a maximum of 18% of the body length in our largest larva. Ossification is initiated in 4-mm larvae and the full complement of I, 5 rays is present at 6.0-mm length.

The hypural anlagen of the caudal fin appear in larvae about 2.5 mm long. They begin to ossify when the larvae reach 4.0 mm and the large superior and inferior elements are well ossified at a length of 6.0 mm. Primary caudal rays begin to ossify in 3-mm larvae and the full complement of 8 + 7 rays is present at about 4.0-mm length. Secondary caudal rays begin ossifying at about 4.0-mm length and there are 5 superior and 5 inferior rays present in our largest stained specimen (6.0 mm).

The dorsal and anal fins begin to develop simultaneously in larvae about 4.0 mm long. Ossification is initiated immediately thereafter and the larvae larger than 5.3 mm have III, 5 anal rays and XII, 8 dorsal rays.

The larvae of *Scorpaena* Type A differ from those of *S. guttata* chiefly in the pattern of melanophores. As in early larvae of *S. guttata*, those of *S.* Type A have melanophores along the dorsolateral surfaces of the gut, along the ventral midline of the tail, and on the pectoral fins. The particular arrangement of melanophores on the tail and pectoral fins is distinctly different in the two forms and is a useful means of separating them. In Type A larvae the ventral midline series extends along the entire length of the tail from above the anus posteriad to the hypural anlage of the caudal fin. In larvae of *S. guttata*, the series is confined to the posterior half of the tail. Accordingly, there are more melanophores in this series in Type A; the range for preflexion larvae is 8 to 14 and for larvae undergoing flexion is 4 to 8. Ventral tail melanophores are not present in postflexion larvae. The melanophore pattern of the pectoral fin is similar in larvae of *S.* Type A and *S. guttata* up to about 3.0 mm in length. At that size, a region of darker pigmentation develops at the ventral aspect of the fin in Type A. This area of darker pigment remains detectable from the surrounding pigment in larvae up to about 6.0 mm in length. This pigment does not develop in larvae of *S. guttata*. As in *S. guttata*, pigment begins to develop on the medial surface of the fin base at about 3.0 mm in length and intensifies during the remaining larval period. In Type A larvae of about 4.0-mm length the dorsal and upper posterior margins of the fin begin to lose melanophores. This clearing becomes more extensive with further development and in the largest larvae the membranes of the most dorsal three rays and the posterior one-third of the fin are clear. In *S. guttata* only a

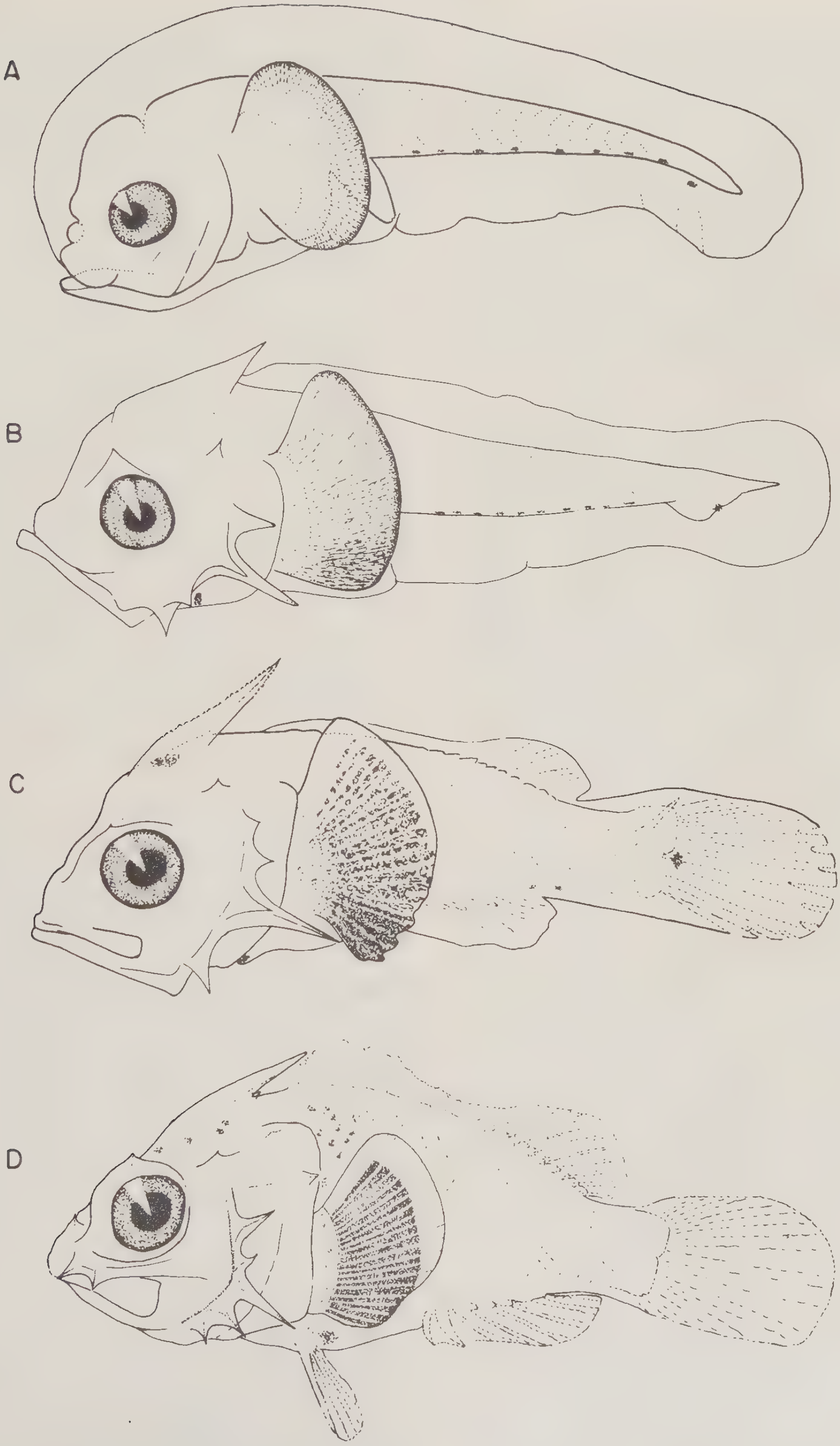

Figure 33.—Larvae of *Scorpaena* Type A. A. 2.5 mm; B. 3.5 mm; C. 4.6 mm; D. 8.0 mm.

narrow portion of the distal region of the fin becomes clear in mid- and late-stage larvae.

Other pigmentation is not substantially different from that of *S. guttata* and other known *Scorpaena* larvae. A melanistic blotch appears just anterior to the junction of the cleithra at about 3.0-mm length and remains throughout the larval period. Melanophores form posteriorly on the brain when the larvae are about 4.0 mm long. At about 5.5 mm, one or two melanophores appear above the olfactory lobes. In 7-mm larvae additional melanophores form above the optic lobes and at 8.0 mm the brain is covered. At 4.0-mm length an embedded melanophore forms at the nape and remains throughout the larval period. Myoseptal pigment is present in the epaxial musculature above the pectoral fin in the 8.0-mm larva.

Distribution.—Most of our larvae of *Scorpaena* Type A were collected on the CalCOFI cruise in the Gulf of California during June 1957. They occurred at 24 stations distributed throughout the entire Gulf (Fig. 34). They occurred at two stations of the CalCOFI cruise during August 1957, however, only a small portion of the plankton from that cruise was sorted and the larvae may have occurred more extensively on that cruise. Except for one station, where the standardized number of larvae was 143, the larvae occurred in small numbers. Eliminating that station the mean number of larvae for the other 25 stations in the Gulf was 12. The species that produces larvae of *Scorpaena* Type A is a summer spawner since no larvae were taken on the December, February, or April cruises in the Gulf during 1956 and 1957.

Larvae of *Scorpaena* Type A occurred at two stations of the EASTROPAC expedition in the vicinity of Panama Bay and at two stations of the Scripps Tuna Oceanography Cruise 58-1, one near Panama Bay and one off the Tres Marias Islands (lat. 21°30′N, long. 106°30′W). The low incidence of these larvae on these wide-ranging expeditions probably reflects the near-shore nature of spawning in the species producing the larvae.

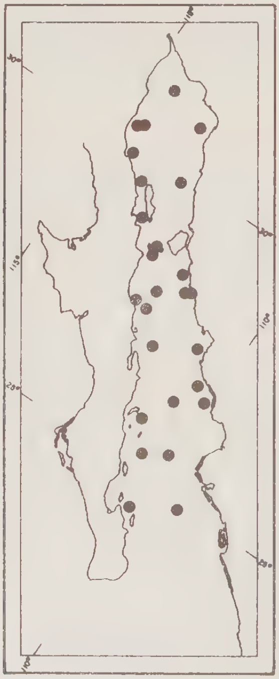

Figure 34.—Stations at which larvae of *Scorpaena* Type A were taken on CalCOFI cruises in the Gulf of California during 1956 and 1957.

Pontinus Poey

Literature.—The literature contains no descriptions or illustrations of the developmental stages of *Pontinus*.

The taxonomy of *Pontinus* in the eastern Pacific is poorly known. At present there are five recognized and six nominal species, however, unpublished information of W. Eschmeyer (Calif. Acad. Sci.) indicates that the species complement of eastern Pacific *Pontinus* is more than double the presently recognized number. In fact, a previously undescribed but abundant species was discovered while examining museum specimens during the present study. Unfortunately, the characters that separate this host of species are mostly not the kind that may be traced backward into larval series.

Distinguishing features.—Larvae of *Pontinus* can be separated from those of other eastern Pacific genera by a combination of characters. As in larvae of *Scorpaenodes* and *Ectreposebastes*, *Pontinus* larvae lack the melanistic shield that covers the dorsolateral surfaces of the gut in *Sebastes*, *Sebastolobus*, and *Scorpaena*. In place of this, larvae of *Pontinus*, *Scorpaenodes*, and *Ectreposebastes* have a deeply embedded medial blotch just dorsal to the axilla. This blotch later enlarges to cover the dorsal surface of the gas bladder. *Pontinus* larvae differ from *Scorpaenodes* in several characters. In *Pontinus*, a single elongate spine develops at the terminus of each parietal ridge. In midstage larvae a small subjacent nuchal spine develops posterior to each parietal spine and remains inconspicuous throughout the larval period. This contrasts greatly with the bifurcate terminus of the parietal ridge in *Scorpaenodes*. The pectoral fins of the two genera differ in shape, relative length, and pigment pattern. They are aliform in *Pontinus* and fan-shaped in *Scorpaenodes*. The pectorals are shorter in *Pontinus*; pectoral fin length averages 31% of the body length in postflexion larvae of Type A and 27% in *Pontinus* Type B; mean length was 39% in postflexion larvae of *S. xyris*. The pectoral fin base is also narrower in *Pontinus*; the depth of the fin base averages 14% of the body length in postflexion larvae of Type A and 16% in *Pontinus* Type B. Fin base depth averaged 18% in postflexion *S. xyris* larvae. Pigmentation of the pectoral fins is limited to the distal margin of the pectoral fin in *Scor-*

paenodes whereas in *Pontinus* the pattern of pigmentation is more complex and develops through sequential stages. Larvae of *Ectreposebastes* are highly distinctive and may be separated from those of *Pontinus* on the basis of body depth and pectoral fin length. Body depth averages 46% of body length for postflexion larvae of *Ectreposebastes* and 39% for postflexion larvae of *Pontinus* Type A. The pectoral fin extends to the base of the caudal fin in *Ectreposebastes* and extends only to the midregion of the anal fin in *Pontinus*. Also, pigmentation of the pectoral fin is markedly different as evident in the illustrations of larvae of the two genera.

Despite the large species complement of *Pontinus*, we can distinguish only three larval forms in our collection. We have a complete larval series of the abundant form, here called *Pontinus* Type A. It ties in with the juveniles of a common but undescribed species of *Pontinus* discovered in this study. A second, much less abundant form, called *Pontinus* Type B, is distinguishable down to a length of about 5.0 mm. Its largest pelagic juveniles have a pigment pattern similar to the smallest known benthic juveniles of *Pontinus sierra* (Gilbert) and it is likely that *Pontinus* Type B is *P. sierra*. A third form, here called *Pontinus* Type C, is known from a few small larvae and is presently not identifiable.

Since larvae of *Pontinus* have not been previously described, a detailed description of *Pontinus* Type A is given below along with a brief description of Type B.

Pontinus Type A, Figure 35

Literature.—None.

Distinguishing features.—The smallest larva available to us is a specimen 2.3 mm long that has no yolk sac. When the larvae reach about 15 mm, pigment saddles begin to form dorsally on the trunk. Although there is no associated abrupt morphological change we have designated this as the beginning of the pelagic juvenile stage. This stage is protracted in *Pontinus* Type A, our largest pelagic specimen being 27.4 mm long. Apparently, there is a large size range over which *Pontinus* Type A pelagic juveniles may become demersal since bottom-caught specimens as small as 17.2 mm are present in our collections.

Larvae of *Pontinus* Type A are deep-bodied. Body depth increases from a minimum of 25% of the body length in the smallest larva to 33% at notochord flexion (Table 36). Body depth averages 39% in postflexion larvae and pelagic juveniles. In small benthic juveniles, average body depth is reduced slightly to 36% of the body length.

The gut is compact in small larvae of *Pontinus* Type A and undergoes a relative lengthening throughout the larval period. Snout-anus distance averages 48% of the body length before notochord flexion, 54% during flexion, and 61% following flexion. In pelagic and small benthic juveniles, snout-anus length averages 64% of the body length.

Table 36. Measurements (mm) of larvae of Pontinus Type A. (Specimens between dashed lines are undergoing notochord flexion.)

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-anal fin distance
2.3	1.0	0.67	0.20	0.24	0.58	0.41	0.36	-	-
2.7	1.2	0.70	0.19	0.24	0.73	0.49	0.40	-	-
3.0	1.6	1.0	0.30	0.31	0.96	0.55	0.45	-	-
3.4	1.7	1.0	0.33	0.30	1.0	0.65	0.50	-	-
4.1	2.2	1.3	0.52	0.40	1.4	1.1	0.65	0.10	2.4
4.6	2.5	1.5	0.63	0.46	1.5	1.2	0.70	0.24	2.8
5.2	3.0	2.0	0.70	0.62	2.0	1.4	0.85	0.84	3.2
5.5	3.5	2.4	0.95	0.56	2.2	1.6	0.86	0.73	3.6
5.9	3.8	2.6	0.90	0.56	2.4	1.8	0.86	1.0	3.8
6.4	3.8	2.5	0.85	0.65	2.6	1.8	1.0	1.2	3.8
6.7	4.0	2.6	0.95	0.68	2.6	2.0	1.0	1.3	4.2
7.1	4.1	2.7	1.0	0.72	2.7	2.1	1.1	1.2	4.2
7.5	4.4	2.9	1.1	0.75	2.8	2.2	1.1	1.4	4.5
8.0	4.8	3.1	1.0	0.84	3.2	2.4	1.1	1.6	5.0
8.6	5.1	3.4	1.0	0.91	3.4	2.7	1.2	1.8	5.5
9.2	5.5	3.5	1.0	0.95	3.6	2.8	1.2	1.8	5.7
9.8	6.0	4.2	1.2	1.0	3.7	2.8	1.2	2.0	6.2
10.6	6.3	4.2	1.2	1.2	3.8	3.8	1.5	2.5	6.5
11.2	7.3	4.8	1.6	1.2	4.7	3.9	1.6	2.8	7.5
12.2	7.5	4.8	1.4	1.5	4.4	4.1	1.6	2.6	8.1
13.2	8.1	5.2	1.5	1.5	5.1	4.2	1.8	2.9	8.7
14.4	8.8	5.8	1.7	1.8	5.3	4.3	1.9	3.3	9.5
*15.0	9.7	6.0	1.8	1.8	6.0	5.3	2.0	3.6	10.1
*16.4	10.0	6.2	1.8	1.8	6.5	5.4	2.2	3.3	10.5
*17.7	11.2	7.3	2.1	1.9	7.2	6.1	2.4	3.9	11.7
*19.6	12.7	7.8	2.1	2.1	8.0	6.7	2.6	4.2	13.4
*21.3	13.7	8.8	2.7	2.3	8.0	6.7	2.7	4.3	14.4
*23.0	14.7	9.6	2.7	2.6	8.3	7.6	2.8	4.6	15.5
*25.7	16.4	10.1	3.2	2.9	9.5	7.9	3.2	4.8	17.2
*27.4	17.9	11.7	3.2	2.6	9.8	8.8	3.3	5.1	19.3
**17.2	10.6	6.9	1.8	1.9	6.2	5.9	2.2	3.8	11.7
**18.9	12.2	7.5	2.1	2.2	6.7	5.7	2.4	4.2	12.8
**20.8	13.0	8.2	2.2	2.4	7.4	6.8	2.6	5.0	14.0
**24.5	16.0	9.8	2.9	2.7	8.8	7.5	3.0	5.2	17.4

*Pelagic juvenile.

**Benthic juvenile.

The head is large in *Pontinus* Type A larvae. Head length increases from a mean of 30% of the body length in preflexion larvae to 32% in larvae undergoing notochord flexion, and averages 40% in postflexion larvae and in pelagic and small benthic juveniles. The moderately small eyes undergo a relative diminution during the larval period. Eye diameter averages 32% of head length before and during notochord flexion and is reduced to a mean of 27% in postflexion larvae and pelagic juveniles. Eye diameter increases slightly to a mean of 28.5% of head length in newly transformed benthic juveniles. Snout length increases from a mean of 32% of head length in preflexion larvae to a mean of 41% in larvae undergoing flexion. Thereafter the mean decreases to 33% in postflexion larvae and to 29% in pelagic juveniles.

The pectoral fins are prominent in the smallest larvae in our collection. At this stage they have a slight aliform shape; however, during later larval stages they become distinctly aliform. Fin length increases from an average of 20% of the body length in preflexion larvae to 26% in larvae undergoing notochord flexion, and to 32% in postflexion larvae and pelagic and small benthic juveniles. The depth of the pectoral fin base is not as great as in other eastern Pacific scorpaenine genera but is greater than in sebastine genera. It decreases from an average of 16% of the body length before and during notochord flexion, to 14% in postflexion larvae and 13% in pelagic and early benthic juveniles. Sequence of ossification of fin elements was not analyzed because only a few larger larvae could be properly stained. Apparently calcium in the larvae leached out in preservative. Pectoral ray counts for nine stained specimens ranged from 17 to 19.

The dorsal, anal, and pelvic fins begin to develop in larvae about 4.0 mm long. The counts for the nine stained specimens were D. XII, 9; A. III, 5; P. I, 5. Hypural anlagen of the caudal fin are visible in the smallest larvae;

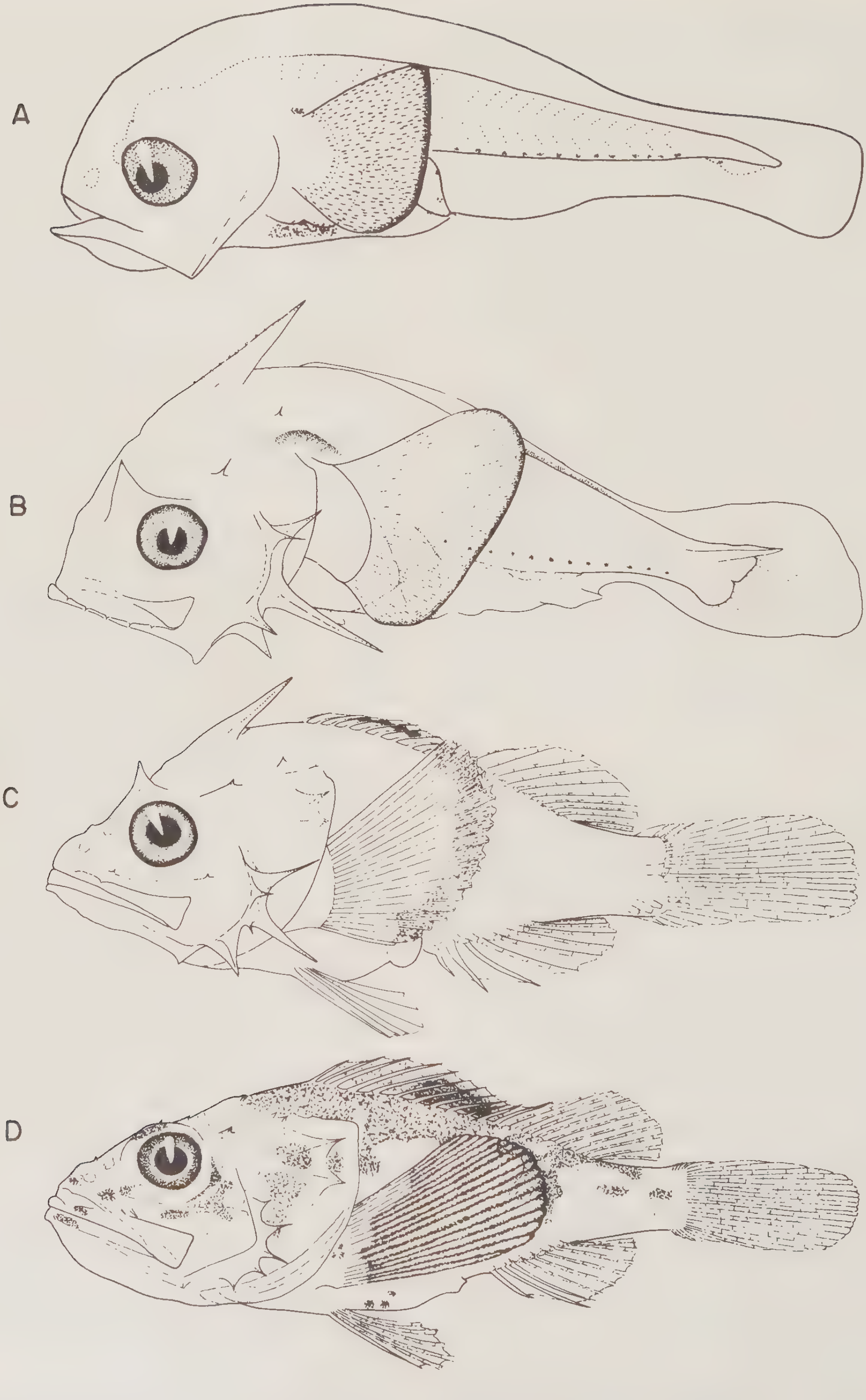

Figure 35.—Developmental series of *Pontinus* Type A. A. 2.3-mm larva; B. 4.1-mm larva; C. 8.0-mm larva; D. 24.5-mm benthic juvenile.

the adult complement is 3 + 2 hypurals. The stained larvae had 8 + 7 principal rays and 6 + 6-7 procurrent rays. All stained larvae had 24 vertebrae. Gill rakers ranged from 5 to 6 on the upper limb and 8 to 12 on the lower limb of the first arch. There were 7 branchiostegal rays.

Early larvae of *Pontinus* Type A are sparsely pigmented. The initial melanophore pattern is similar to that of *Scorpaenodes*. A series of 11 to 16 melanophores (mean of 13 ± 1.3 SD for 14 larvae counted) is present along the ventral midline of the tail. The series extends from the anus posteriad to the hypural anlage of the caudal fin. A wider space separates the ultimate melanophore from the others. The number of melanophores and their spacing is similar in *Scorpaenodes xyris* except that in that species the series extends farther anteriad to the point of divergence of the terminal section of the gut. In *Pontinus* Type A larvae the ventral tail melanophores begin to become embedded during notochord flexion and are not visible in larvae larger than 6.0 mm.

Other pigment present initially is a medial blotch anterodorsad to the axillary region. With further development this expands to form a shield over the gas bladder. It becomes progressively less visible with thickening of the trunk musculature. Similar pigment is present in *Scorpaenodes* and *Ectreposebastes*.

Pigment is present initially on the gut as a few faint melanophores along the dorsal surface of the preterminal section of the gut and as a streak along the ventral midline, with heaviest concentration below the liver. Also, fine melanophores are present along the edge of the finfold just anterior and posterior to the anus. These areas of pigmentation persist in larvae up to about 5.5 mm in length and are present thereafter. When the larvae reach about 10.0 mm in length, large melanophores begin to appear internally on the perivisceral membrane and, with further development, eventually cover the entire membrane.

The other pigmentation present initially is on the pectoral fins. Minute melanophores cover the entire blade of the fin and are present at the margin of the medial surface of the fin base. This contrasts with the pattern in early larvae of *Scorpaenodes* which have, at most, the distal half of the fin blade covered with melanophores and which have none on the fin base. The pattern of pigmentation on the pectorals of *Pontinus* Type A goes through a series of distinct changes as larval development proceeds. Towards the end of notochord flexion the melanophores disappear from the fin base and begin to recede from the basal region of the fin blade. The basal clear area continues to enlarge and, at maximum recession in larvae of about 10 mm in length, pigment is reduced to the distal margin. At about 10.0 mm the distal band begins to expand and becomes progressively wider during the remainder of the larval period and pelagic juvenile phase. At the end of the pelagic juvenile stage only a small portion of the fin remains unpigmented. Newly transformed benthic juveniles have a mottled pattern on the fins with a prominent dark blotch near the base.

In larvae about 6.5 mm long, a melanistic blotch appears on the membrane between the 3rd and 4th spinous rays of the dorsal fin. Additional blotches appear anterior and posterior to this as development proceeds, and larvae larger than 7.0 mm have a series of blotches from the 2nd and 3rd interradial membrane to the 5th or 6th membrane. In pelagic juveniles the entire membrane of the spinous dorsal fin becomes pigmented; however, a much darker blotch is present between the 6th and 11th spines. This dark blotch persists in benthic juveniles.

Melanophores appear on the brain in 10-mm larvae, initially with a single pigment spot above each optic lobe. Others form rapidly and the entire dorsal surface of the brain is covered in larvae larger than 13.0 mm.

Saddles of melanistic pigment begin to form on each side of the dorsal midline in 13-mm larvae, one between the 1st and 2nd dorsal spines, and the other between the 5th and 7th spines. These enlarge to include the regions between the 1st and 3rd dorsal spines and the 5th and 10th spines in larvae larger than 15.0 mm. Two other pigment saddles appear in pelagic juveniles, one below the soft dorsal fin and the other at the caudal peduncle. In the largest pelagic juveniles, the anterior pigment saddle covers the nape, the large one posterior to it bifurcates and extends ventrad to the horizontal septum, the one below the soft dorsal extends ventrad to the base of the anal fin, and the one at the peduncle is a weak band. These markings break up into a more complex pattern in benthic juveniles.

Pigmentation appears on other regions in pelagic juveniles. At about 15.0-mm length, a blotch forms at the midregion of each pelvic fin and the entire membrane of the fin is pigmented at about 20.0-mm length. When pelagic juveniles reach about 25-mm length, a blotch appears at the midregion of the soft dorsal and the soft anal fin. These appear as extensions of the prominent trunk band in benthic juveniles.

The head becomes pigmented in pelagic juveniles first on the opercle and on the region above the opercle. At the end of the pelagic phase, the entire lateral aspect of the head is mottled.

Distribution.—The midwater trawl and plankton collections of CalCOFI, EASTROPAC, and the STOR group show the geographic distribution of larvae and pelagic juveniles of *Pontinus* Type A (Fig. 36). CalCOFI plankton collections show that larvae and pelagic juveniles of *Pontinus* Type A occur in the Gulf of California up to about lat. 28°N. On the outer coast of Baja California, pelagic juveniles of *Pontinus* Type A have been taken as far north as Punta Eugenia (about lat. 28°N). Collections of the EASTROPAC expedition and STOR show that larvae and pelagic juveniles occur southward to the northern coast of Peru (about lat. 5°S). It has an extensive distribution in the Gulf of Panama and westward to the Galapagos Islands. In general, its distributional pattern is similar to that of *Scorpaenodes xyris* except that *Pontinus* Type A is more abundant in offshore regions along the tropical American coast. Larvae occurred in small numbers in both CalCOFI and

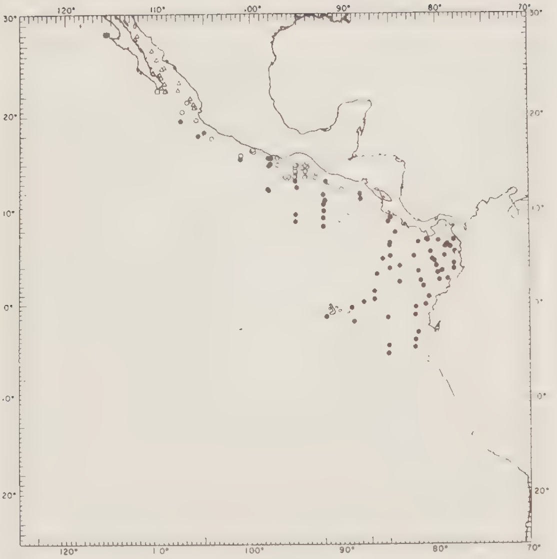

Figure 36.—Stations at which larvae and pelagic juveniles of *Pontinus* Type A were collected on CalCOFI cruises (triangles) during 1956 and 1957, EASTROPAC expeditions (closed circles) during 1967 and 1968, and Scripps Tuna Oceanography cruises (open circles) during 1958 and 1959. Open square represents a station from the Scripps Institution of Oceanography fish collection and closed square a station from the University of California, Los Angeles, fish collection.

EASTROPAC plankton tows. The mean number of specimens for all plankton tows was 3.4 ± 6.36 SD with a range of 1 to 34; 50% of all plankton tows had only a single specimen.

In the tropical waters surveyed during the EASTROPAC expedition, the number of occurrences was about equal on the winter cruises (February to April) and the summer cruises (July to September).

***Pontinus* Type B, Figure 37**

Literature.—None.

Distinguishing features.—The smallest larva available is a 5.0-mm specimen undergoing notochord flexion. Dorsal pigment saddles are already beginning to form at this size, and well-formed saddles are present in specimens as small as 10 mm. In *Pontinus* Type A the pigment saddles begin to form at about 15 mm, a size chosen for convenience as the beginning of the pelagic juvenile stage. Since pigment saddles begin to form in midstage larvae of *Pontinus* Type B it is more appropriate to consider the appearance of scales at about 10 mm as the event marking the beginning of the pelagic juvenile stage. The largest pelagic juvenile in our collection is 23.1 mm. The size at transformation into benthic juveniles is not known since the smallest benthic juvenile of *Pontinus* Type B in our collection is 29.0 mm.

The smallest larva in our collection, 5.0 mm long, has almost completed notochord flexion indicating that notochord flexion is probably initiated in 4-mm larvae. At 6.0 mm, notochord flexion is completed. Notochord flexion occurs at a smaller size in larvae of *Pontinus* Type A and is completed when the larvae reach about 5.0-mm length.

Larvae of *Pontinus* Type B are deeper-bodied than those of *Pontinus* Type A. Body depth at the pectoral fin base in *Pontinus* Type B larvae undergoing notochord flexion is 45 to 46% of the body length (Table 37). In postflexion larvae the mean is 43%, and in pelagic juveniles it is 41%. The more slender-bodied larvae of *Pontinus* Type A show an opposite trend. Body depth increases from a mean of 33% of the body length in larvae undergoing notochord flexion to a mean of 39% for postflexion larvae and pelagic juveniles.

The compact gut is already masked by trunk musculature in the smallest larva in our collection. Snout-anus length is relatively longer in *Pontinus* Type B than in *Pontinus* Type A. It averages 64% of the body length in *Pontinus* Type B larvae undergoing notochord flexion and 67% in postflexion larvae and pelagic juveniles while in comparable stages of *Pontinus* Type A the means are 54% and 62%.

The head is larger in *Pontinus* Type B than in *Pontinus* Type A. Head length in the former averages 45% of the body length during notochord flexion and in postflexion larvae and 42% in pelagic juveniles. Relative head length shows an opposite trend in *Pontinus* Type A, averaging 32% in larvae undergoing flexion and 40% in postflexion larvae and pelagic juveniles. The eye is relatively larger in *Pontinus* Type B compared with *Pontinus* Type A; eye diameter averages 32% of head length for larvae and pelagic juveniles of the former and 27% in comparable stages of *Pontinus* Type A. Snout length is relatively shorter in *Pontinus* Type B compared with *Pontinus* Type A. In the former it averages 30% of the head length in larvae undergoing notochord flexion, 28% in postflexion larvae, and 24% in pelagic juveniles. At comparative stages of *Pontinus* Type A it averages 41%, 33%, and 29% of the head length.

Pectoral fin length averages 33% of the body length in *Pontinus* Type B larvae undergoing notochord flexion and 27% in postflexion larvae and pelagic juveniles. In comparable stages of *Pontinus* Type A, fin length

Table 37. Measurements (mm) of larvae of Pontinus Type B. (Specimens between dashed lines are undergoing notochord flexion.)

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-anal fin distance
5.0	3.0	2.2	0.70	0.65	2.3	1.7	0.85	0.96	3.0
5.5	3.8	2.5	0.73	0.70	2.5	1.8	1.0	1.0	3.8
6.0	4.0	2.8	0.82	0.78	2.8	1.8	1.1	1.2	4.0
8.7	5.9	3.8	0.98	1.2	3.5	2.1	1.2	1.7	6.0
*10.5	7.0	4.8	1.3	1.5	4.2	2.9	1.6	2.2	7.4
*11.2	7.7	4.7	1.1	1.6	4.7	2.7	1.7	2.1	8.2
*12.7	8.5	5.7	1.4	1.8	5.2	3.5	1.8	2.7	9.1
*13.7	9.5	5.8	1.4	1.9	5.8	3.9	1.9	2.8	10.0
*14.0	9.5	6.2	1.7	2.2	5.4	4.0	1.8	3.0	10.0
*15.4	10.0	6.2	1.5	2.2	6.2	4.4	2.1	3.3	10.6
*17.1	11.3	6.7	1.5	2.5	7.2	4.6	2.3	3.8	11.8
*22.0	13.5	8.8	1.9	2.9	8.8	6.2	2.9	4.3	14.7
*23.1	14.9	9.6	2.2	3.3	9.0	6.2	2.9	4.8	15.9

*Pelagic juvenile.

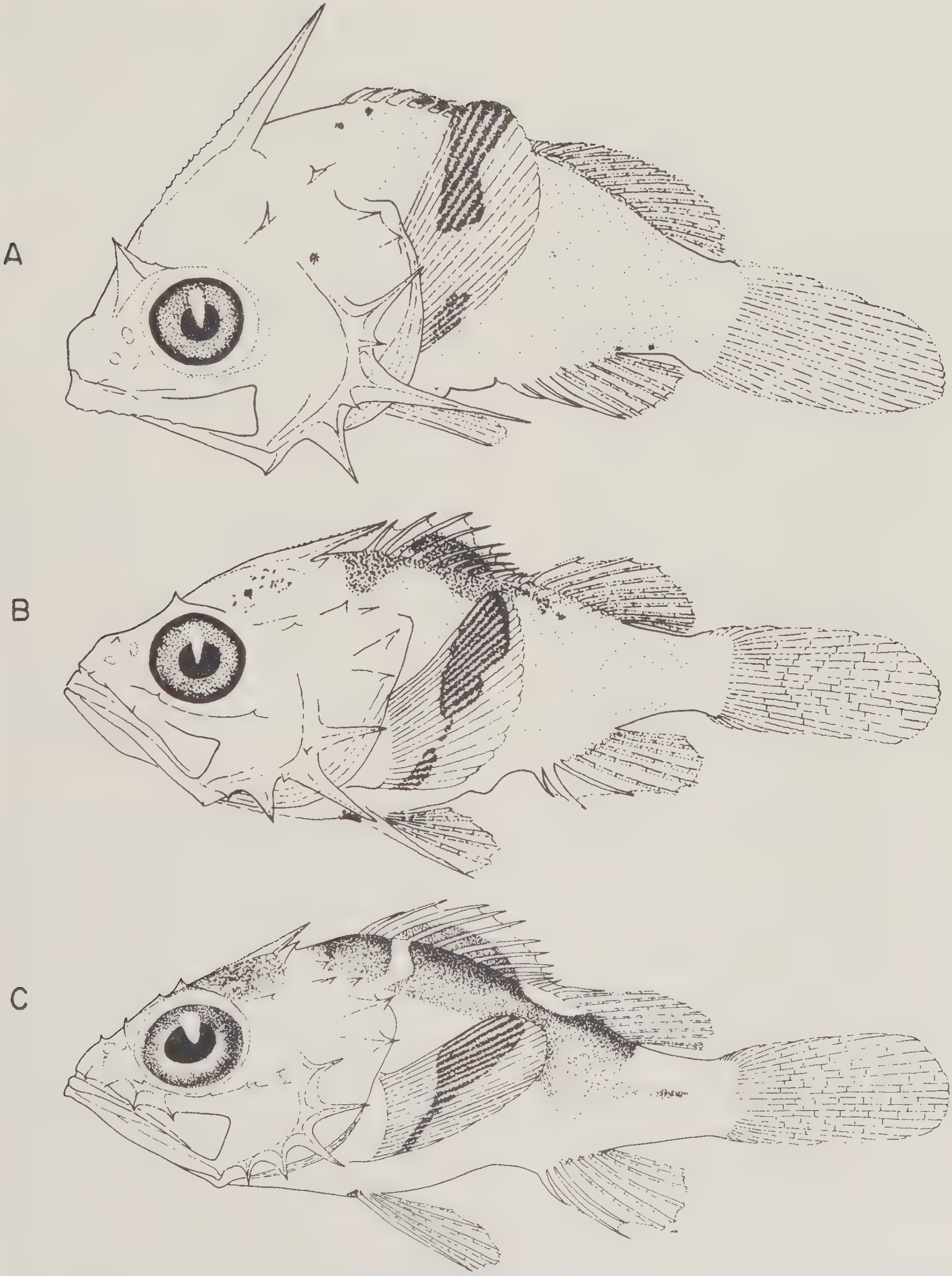

Figure 37.—Developmental series of *Pontinus* Type B. A. 5.0-mm larva; B. 8.7-mm larva; C. 15.4-mm pelagic juvenile.

averages 26% and 32%, respectively. The pectoral fin base is slightly deeper in *Pontinus* Type B compared with *Pontinus* Type A and like the latter becomes relatively shallower as development proceeds. The fin base averages 17% of the body length in *Pontinus* Type B larvae undergoing notochord flexion, 16% in postflexion larvae, and 14% in pelagic juveniles. In comparable stages of *Pontinus* Type A, the averages are 15%, 14%, and 13%. The shape of the fin in *Pontinus* Type B is aliform as it is in *Pontinus* Type A. The sequence of ossification of fin elements and rays could not be determined because of calcium leaching in the small larvae during preservation and storage. In six larger larvae and pelagic juveniles which were stained, all had 18 pectoral rays. The dorsal, anal, and pelvic fins were well formed in the smallest larvae available. The counts of the stained specimens were D. XII, 9; A. III, 5; P. I, 5. Three superior and two inferior hypural elements develop in the caudal fin; there are 8 + 7 principal and 5-7 + 5-7 procurrent rays. All stained larvae had 24 vertebrae. Gill rakers of the stained pelagic juveniles ranged from 5 to 6 on the upper limb and 9 to 11 on the lower limb of the first arch. There were 7 branchiostegal rays.

The absence of specimens of *Pontinus* Type B smaller than 5.0 mm precludes knowledge of the pigment pattern of early larval stages. Pigmentation of larvae larger than this and pelagic juveniles is similar to that in larvae and pelagic juveniles of *Pontinus* Type A, but there are distinctive differences that allow separation of the two forms.

Several melanophores are present at the ventral midline posterior to the developing anal fin. These remnants of the ventral midline series are not found in larvae larger than 8.7 mm. Another component of the original pigment pattern, the melanistic shield covering the gas bladder, is already masked by trunk musculature in the 5.0-mm larva and becomes further embedded with continued development.

The pattern on the pectoral fins is markedly different from that on the fins of *Pontinus* Type A larvae. On the 5.0-mm specimen a pigment streak extends obliquely ventrad from the dorsal tip of the fin blade to the midregion of the fin. Also, a small blotch is present along the base of the six most ventral rays and one is present on the medial surface of the fin base in this region. The medial blotch is not present in larvae larger than 6.0 mm; however, the ventral blotch at the base of the fin blade extends dorsad with further development and ultimately connects with the dorsal streak to produce a complete bar in larvae longer than 10.0 mm. This oblique bar remains a prominent feature throughout the larval and pelagic juvenile stages. Other fin pigment present in the 5.0-mm larva is a patch of melanophores at the base of each pelvic fin. It remains in larger larvae and in pelagic juveniles.

Pigment is also present in 5-mm larvae on the spinous dorsal fin. The blotch on the spinous dorsal membrane extends from the 3rd or 4th spine to the 6th, 7th, or 8th spine and remains throughout later developmental stages. It enlarges slightly with development and covers the membrane from the 1st to 10th rays in the 23.1-mm pelagic juvenile. A portion of this blotch from the 6th to 10th ray is darker than the background and stands out as a black spot. This same pattern is present on the spinous dorsal fin of a 39.0-mm benthic juvenile of *P. sierra*.

The dorsal pigment saddles appear much earlier than in larvae of *Pontinus* Type A and are distinctly different in form. In 5-mm larvae of *Pontinus* Type B, small blotches are present on either side of the dorsal midline at the anterior end of the spinous dorsal fin and at the posterior region of the fin. In 8-mm larvae the anterior saddle has enlarged to occupy the region along the anterior one-third of the spinous dorsal and has enlarged ventrad to the head and forward over the nape. A narrow space separates the anterior saddle from the posterior saddle which now extends along the posterior two-thirds of the spinous dorsal and ventrad about halfway to the lateral line. A third pigment saddle is beginning to form on either side of the soft dorsal fin. In 10-mm larvae the posterior saddle of the spinous dorsal fin extends to the lateral line and the one at the soft dorsal extends to the horizontal septum. In 14-mm larvae the latter saddle extends ventrad to the anal fin where it meets a blotch of pigment on the membrane of the soft anal rays. Anterior to this bar three distinctive blotches lie along the horizontal septum. At about 17 mm a blotch forms on each side of the caudal peduncle, and in the largest pelagic juvenile (23.1 mm) it has connected with dorsal midline pigment to form a saddle. Also, in this largest specimen a blotch is present over each side of the hypural region. The pattern of pigment saddles and blotches in the largest pelagic juveniles matches closely the pattern found in a 39.0-mm benthic juvenile of *P. sierra*.

Head pigment first appears in 8-mm larvae on the dorsal and lateral surfaces of the brain and remains throughout the larval period. In 10-mm larvae, pigment appears along the basal region of the branchiostegal rays and on the posterior region of the opercle. Also, a blotch of pigment is present on the cheek ventroposterior to the eye. In the largest pelagic juvenile additional pigment appears anterior to the eye.

Distribution.—*Pontinus sierra* is known to range from the Gulf of California to Peru. Pelagic juveniles of *Pontinus* Type B were taken on two midwater trawl stations in the southern Gulf of California and on a single midwater trawl station on the outer coast between Magdalena Bay and Cape San Lucas (Fig. 38). A wide latitudinal gap separates these occurrences from the remainder of the pelagic juveniles and larvae which were taken off the Central and South American coasts, as far south as the equator. They appear to be more restricted to coastal waters than are larvae and pelagic juveniles of *Pontinus* Type A and there were no occurrences at the Galapagos Islands.

Larvae and pelagic juveniles of *Pontinus* Type B are rare compared to catches of *Pontinus* Type A. Of the 23 total positive hauls, 17 contained a single specimen and 6 contained two specimens.

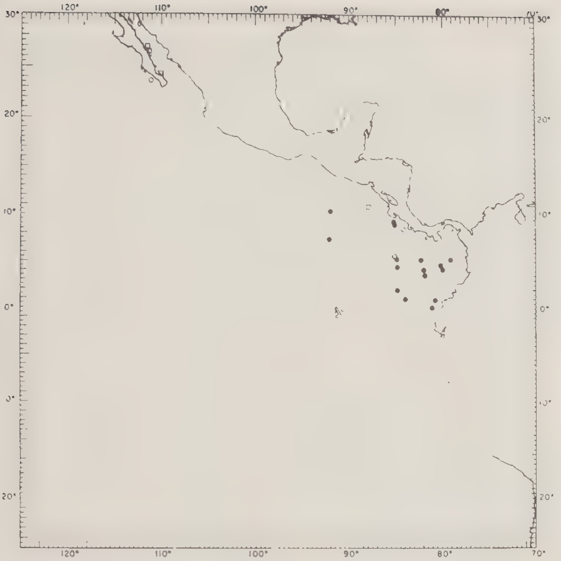

Figure 38.—Collections of larvae and pelagic juveniles of *Pontinus* Type B from various sources. Open circles, Scripps Tuna Oceanography cruises, closed circles, EASTROPAC Expedition; open squares, Scripps Institution of Oceanography fish collection.

Ectreposebastes Garman

Literature.—In their review of the scorpaenid subfamily Setarchinae, Eschmeyer and Collette (1966) gave a brief description of two larval specimens (15 and 16 mm SL) of *E. imus.* Illustrations of the larvae have not appeared in the literature.

Distinguishing features.—Larvae of *Ectreposebastes* can be distinguished from those of other eastern Pacific scorpaenid genera by a combination of characters. They have enormous pectoral fins. The depth of the fin base is 19 to 22% of the body length while in the larvae of other tropical scorpaenid genera, except *Scorpaenodes*, it ranges from 12 to 18% of the body length. In *Scorpaenodes*, the depth of the pectoral fin base ranges from 16 to 21% of the body length over most of the larval period. Larvae of *Scorpaenodes* have a bifurcate parietal ridge whereas *Ectreposebastes* larvae have a spikelike spine at the terminus of each parietal ridge. Also, the pectoral fins of *Ectreposebastes* are longer than in other scorpaenid genera. In larvae which have completed notochord flexion, the pectorals reach or extend beyond the base of the caudal fin. Also, larvae of *Ectreposebastes* are deeper-bodied than other scorpaenid genera in the eastern Pacific. The rays of the dorsal and anal fins are highly elongate and the pterygiophores and overlying muscles appear to protrude from the body profile. Eschmeyer and Collette (1966) considered *Ectreposebastes* to be a monotypic genus of the tropical Atlantic and Pacific but, in a recent paper, Eschmeyer and Randall (1975) suggested that *E. niger* (Fourmanoir) may be a distinct species. Only a single larval form was recognizable and is herein referred to as *E. imus*.

Ectreposebastes imus Garman, Figure 39

Literature.—As above.

Distinguishing features.—Size at hatching is unknown; the smallest larva in our collection is 2.8 mm. The larvae attain a larger size than any other known species in the family. A 28.2-mm specimen is just beginning to develop juvenile pigmentation on the head.

Larvae of *E. imus* are the deepest- and narrowest-bodied of all known eastern Pacific scorpaenid larvae. Body depth averages 37% of body length in the preflexion larvae and increases gradually thereafter to 55% in the 28.2-mm transforming specimen (Table 38). The gut has a compact anterior mass with a long intestinal section extending posteriad to the anus. Snout-anus distance is large; it averages 53% of the body length in preflexion larvae and increases thereafter to a maximum of 76% in the 23.0-mm specimen.

The head is large and develops a pair of spikelike parietal spines, each with a short posteriorly directed nuchal spine behind it. Head length averages 34% of the body length before and during notochord flexion, and averages 38% at completion of flexion. The eyes are small and undergo a relative diminution during the larval period. Eye diameter averages 32% of head length before and during notochord flexion and is gradually reduced to a minimum of 22% in the 23.0-mm larva. Snout length averages 33% of head length over the entire larval period.

Larvae of *E. imus* have distinctive fins. The pectoral fins are the longest of any known scorpaenid. Pectoral fin length averages 33% of the body length in preflexion larvae, 38% during flexion, and increases to a maximum of 57% of the body length in the transforming specimen. They extend to or beyond the hypural elements in larvae 6.7 mm and longer. Also, the fin base is unusually deep; it ranges from 19 to 22% of the body length during the larval period. Although there were too few larvae in the series to permit staining, the development of fin rays can be observed on unstained specimens. The full complement of 18 to 20 pectoral rays is present in the smallest larva (3.8 mm) in our collection. The pelvic fin is moderate in size and is first apparent in the 5.5-mm larva where its length is 9% of the body length. Fin length increases gradually during the remaining larval period to

Table 38. Measurements (mm) of larvae of *Ectreposebastes imus*. (Specimens between dashed lines are undergoing notochord flexion.)

Standard length	Snout-anus distance	Head length	Snout length	Eye diameter	Body depth	Pectoral fin length	Pectoral fin base depth	Pelvic fin length	Snout-anal fin distance
2.8	1.6	1.0	0.31	0.31	1.0	0.68	0.54	-	-
3.2	1.8	1.1	0.38	0.38	1.1	1.2	0.68	-	-
3.4	1.9	1.2	0.43	0.42	1.4	1.3	0.76	-	-
3.8	1.9	1.2	0.43	0.38	1.4	1.2	0.72	-	-
4.2	2.0	1.4	0.45	0.40	1.5	1.3	0.90	-	2.2
5.5	3.2	1.9	0.65	0.58	2.2	2.1	1.2	0.50	3.2
6.2	3.4	2.2	0.76	0.71	2.5	2.3	1.3	0.66	3.4
6.7	4.2	2.7	0.88	0.80	2.8	3.3	1.5	1.2	4.3
9.8	6.5	3.8	1.2	1.1	4.6	4.2	2.1	2.2	6.7
11.3	7.6	4.5	1.2	1.2	5.4	5.0	2.5	2.5	7.7
23.0	17.6	9.2	2.7	2.0	11.2	11.3	4.4	5.0	17.7
*28.2	19.9	10.1	3.3	2.5	15.5	16.0	5.8	7.9	20.3

*Transforming specimen.

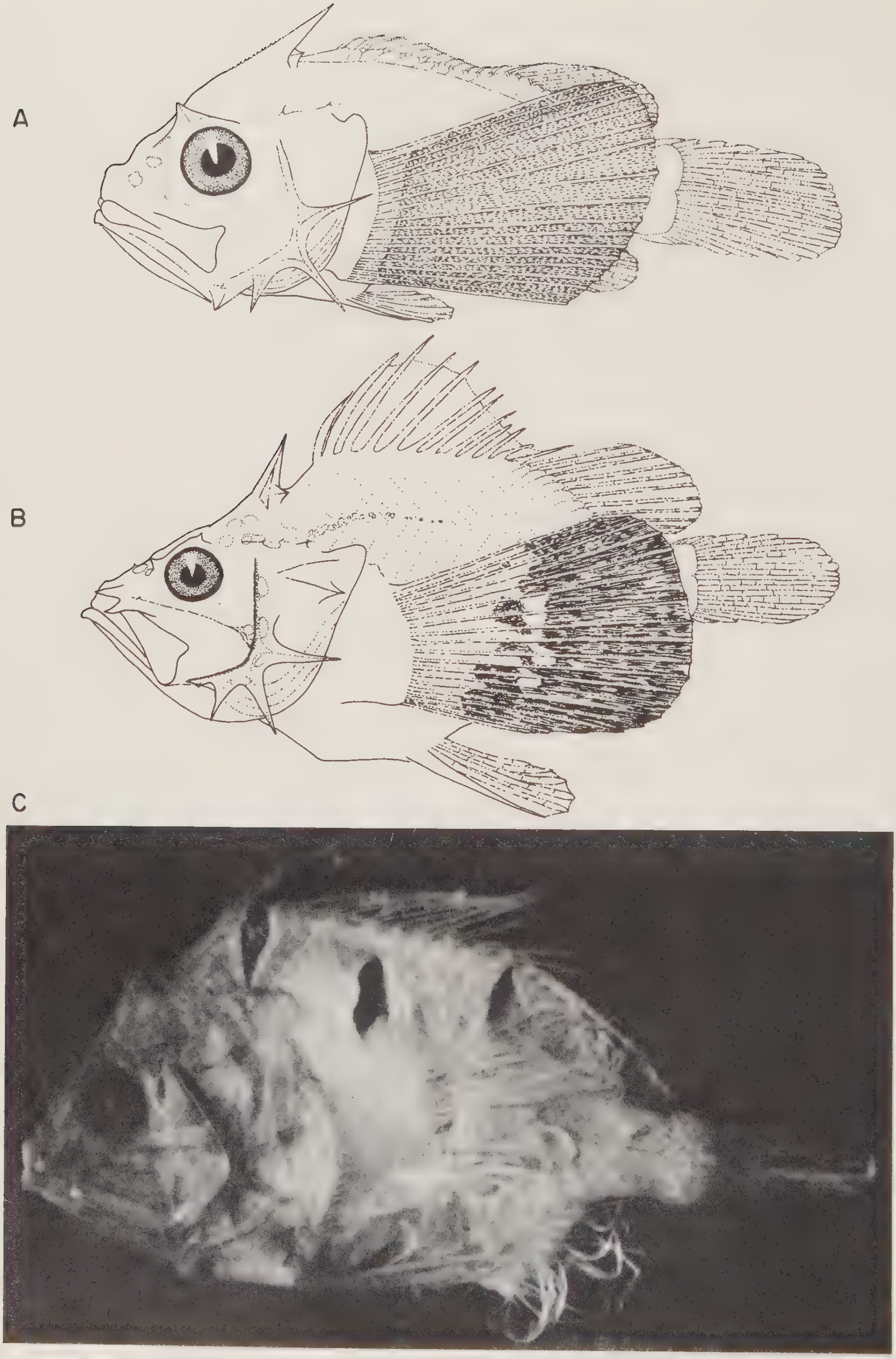

Figure 39.—Developmental stages of *Ectreposebastes imus*. A. 6.7-mm larva; B. 23.0-mm larva; C. 28.2-mm transforming specimen from stomach of *Alepisaurus* (note teeth lacerations).

a maximum of 28% of the body length in the transforming specimen. The full complement of I, 5 pelvic rays is present in the 6.7-mm larva.

The dorsal and anal fins are beginning to develop in the 4.2-mm larva and the full complements of XII, 10(9) dorsal rays and III, 6(5) anal rays are present in the 6.7-mm larva. In the 23.0-mm larva the third dorsal spine is 2.5% of the body length.

The hypural anlagen and the principal caudal rays have begun to develop in the 3.8-mm larva. The full complements of 3 + 2 hypurals and 8 + 7 caudal rays are visible in the 5.5-mm larva. The procurrent rays are beginning to form at 5.5 mm, however, the full complement of 5-6 + 6-7 rays is not present until late in the larval period.

In the smallest larvae, melanistic pigment is present on the dorsal surface of the developing gas bladder, along the ventral surface of the gut, and on the pectoral fins. The series of melanophores along the ventral midline of the tail contains 11 to 14 pigment spots which disappear before the beginning of notochord flexion. The ventral gut pigment is lost before the larvae reach 4.0 mm and that above the gas bladder becomes obscured by trunk musculature. In the smallest larvae, the pectoral fin membrane is covered solidly with small melanophores. When the larvae reach 5.5 mm, there is an unpigmented region at the base of each fin and, with continued development, the melanistic zone becomes more distally located. In the 23.0-mm larva, the distal half of the fin is pigmented and in the transforming specimen the distal third of each fin is pigmented. In the latter specimen, the fine melanophores that will eventually cover the entire body are beginning to appear on the head and upper trunk.

Distribution.—According to Eschmeyer and Collette (1966) and Eschmeyer and Randall (1975), *E. imus* is known from the eastern and western Atlantic, the southeastern Pacific off the Galapagos Islands, and Peru, Hawaii, and Japan. Specimens in this study were taken from about lat. 2° to 6°N off the coast of Colombia and Ecuador, at the equator between long. 100° and 127°W, and at the Hawaiian Islands (Fig. 40). Larvae of *E. imus* are extremely rare in plankton collections. Of the 15 specimens available to us, 8 came from EASTROPAC 1-m plankton hauls, 6 were taken by midwater trawls, and the transitional specimen came from an *Alepisaurus* stomach.

ACKNOWLEDGMENTS

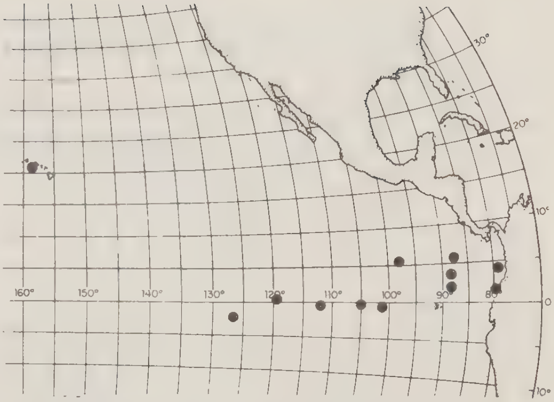

Figure 40.—Collections of larvae of *Ectreposebastes imus* from EASTROPAC expeditions, Scripps Tuna Oceanography cruises, Scripps Institution of Oceanography fish collection, and the University of Hawaii.

This study was facilitated by the generous efforts of many people. For the loan of valuable specimens we are indebted to Robert Lavenberg, Los Angeles County Museum; Richard Rosenblatt, SIO; Erik Bertelsen, University Museum, Copenhagen; George Kelley, Thomas McKenney, and Ruth Stoddard, Northeast Fisheries Center, NMFS; Thomas Clark, University of Hawaii; and C. R. Hitz, Northwest Fisheries Center, NMFS, Seattle. Jerry Newmann, LACM, and Joseph Copp, SIO, provided valuable help in locating and transferring specimens to our laboratory. We thank John Fitch (California Department of Fish and Game, Long Beach) and Carl L. Hubbs and Richard Rosenblatt (SIO) for sharing with us their extensive knowledge of scorpaenid fishes. We are especially indebted to Lo-chai Chen (San Diego State University), William Eschmeyer (California Academy of Sciences), and Jurgen Westrheim (Fisheries Research Board of Canada, Nanaimo) for reviewing the manuscript and offering valuable suggestions for improving it. Eschmeyer's comments were particularly extensive on *Trachyscorpia* and North Atlantic *Sebastes* and were essential to the writing of these sections. From the Southwest Fisheries Center, NMFS, La Jolla, Amelia Gomes and Betsy Stevens provided technical help during the course of the study; George Mattson prepared the illustrations in Figures 1a-c, 2c, 3, 4b, 5, 7, and 24 through 29; and Ken Raymond and Henry Orr drafted Figures 18, 19, 30, 36, and 38. Special thanks goes to John LaGrange and Richard Pleasant for supplying live rockfish larvae and to David Kramer (NMFS, LaJolla) for aiding in the culturing of these larvae. Pamela Moser generously gave her time in typing parts of the manuscript.

This paper is dedicated to the memory of Don Dockins who, as a worker in the fish collection of Scripps Institution, untiring colleague on countless collecting trips, and friend of the senior author, aided greatly in the completion of the paper.

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Wind Stress and Wind Stress Curl Over the California Current

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ABSTRACT

Historical surface marine wind observations are summarized by 1-degree square areas and months to describe the seasonal distribution of wind stress over the California Current. Off the coasts of southern California and Baja California, an alongshore equatorward component of surface wind stress is present throughout the year. The distributions of wind stress north of Cape Mendocino are characterized by marked changes in direction and magnitude between summer and winter. The predominant wind stress maximum shifts northward coherently from off Point Conception in March to south of Cape Blanco in September, and extends approximately 500 km in the offshore direction and 1,000 km in the alongshore direction. Maximum values of surface wind stress occur during July near Cape Mendocino.

The wind stress curl is positive near the coast and negative in the region offshore. A line of zero wind stress curl parallels the coast 200 to 300 km offshore, except off central Baja California. The patterns of wind stress curl are consistent with the existence of an equatorward Sverdrup transport offshore and a poleward transport near the coast.

INTRODUCTION

Spatial variation of surface wind stress has long been recognized as a fundamental quantity in discussions of the wind-driven ocean circulation. Sverdrup's (1947) transport balance relates the vertically integrated meridional mass transport in the interior ocean to the open ocean wind stress curl. Munk (1950) extended the theory to a closed basin and estimated the mass transports for several oceanic circulations from a knowledge of the wind stress alone. Recent theoretical developments have attemped to explain the well-known westward intensification, but have largely ignored the wind-driven circulation in eastern boundary currents, such as the California Current.

The California Current flows southeastward along the west coast of the United States as one branch of the large anticyclonic gyre in the North Pacific Ocean. The predominant surface current occurs between a cell of high atmospheric pressure to the west and a continental thermal low situated over California. Seasonal variations in the direction and strength of the surface wind are related to shifts in location of the high pressure system and intensification of the semipermanent thermal low.

The basic flow of the California Current system may be described in terms of the local wind stress (Reid et al. 1958). The equatorward surface current and poleward undercurrent are typical of eastern boundary currents (Wooster and Reid 1963). Munk (1950) has suggested that the average wind distribution off California is consistent with the existence of an equatorward surface current offshore and a poleward current inshore. However, lack of an adequate data base has precluded a detailed analysis of the relationships among the distributions of surface wind stress, the southward flowing California Current, and the northward flowing countercurrent which appears seasonally off the coasts of California, Oregon, and Washington.

A related phenomenon in eastern boundary currents is the process of coastal upwelling. The role of upwelling in bringing nutrients into the surface layers where they are available for organic production is widely recognized. According to the simplified model (Sverdrup 1938), equatorward wind stress parallel to the coast induces flow in the surface Ekman layer of the ocean which is deflected offshore by the earth's rotation (Ekman 1905). When this occurs over an expanse of coast where horizontal surface flow cannot compensate for that driven offshore, the balance is maintained by upwelling of subsurface water. Smith (1968) suggested that wind stress, being the driving force in this mechanism, may be the most important single variable in coastal upwelling.

Previous estimates of the surface wind stress over the oceans have been based primarily on wind data taken from the U.S. Hydrographic Office Pilot Chart wind roses (Hidaka 1958; Hellerman 1967). The large-scale features evident in these distributions are consistent with the occurrence of the major cyclonic and anticyclonic circulations in the oceans. However, the coarse spatial and temporal resolution of these data (5-degree quadrilateral space average and 3-mo time average) are not adequate to describe the locally driven processes evident in the California Current system.

Wooster and Reid (1963) used Hidaka's estimates of surface wind stress to calculate the offshore Ekman transport and described the locations and seasonal timing of the major coastal upwelling regimes in terms of these "upwelling indices." Bakun (1973) extended the concept of the upwelling index by computing estimates of Ekman transport from routinely available analyzed surface atmospheric pressure fields. Temporal fluctuations are well described by these data. However, both the derived quantities based on Hidaka's wind stress data and Bakun's upwelling indices suffer from an inability to characterize small-scale features of the Ekman transport field, particularly near the coast. For example, where these data may indicate surface divergence on the large scale, smaller scale surface convergence might exist, with associated effects on distributions of organisms within the coastal upwelling zone.

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This report provides more detailed descriptions of the surface wind stress distributions over the California Current. The study differs from previous work by calculating monthly mean values on a 1-degree square area basis. Surface marine wind observations have been utilized in the computations. Roden (1974) evaluated the surface wind stress on a 1-degree latitude-longitude grid. However, Roden's distributions were derived from monthly mean surface atmospheric pressure analyses based on a 5-degree latitude-longitude grid. Thus, any information concerning space scales smaller than 5 degrees is due to the particular interpolation scheme used to refine the data to a 1-degree grid, rather than due to observed data.

The monthly mean data described in this report adequately resolve the seasonal cycle, which is the dominant time scale for coastal upwelling (Mooers et al. 1976). The high resolution in space and time may provide the observational background for more detailed investigations of the relationships among the local wind stress distributions, the equatorward surface current offshore, the poleward surface and subsurface flow inshore, and distributions of certain species of fishes, such as the northern anchovy, *Engraulis mordax*, and the Pacific mackerel, *Scomber japonicus*.

DATA REDUCTION

The monthly mean distributions of surface wind stress presented in Appendix I are based on summaries of data contained in the National Climatic Center's file of surface marine observations (Tape Data Family-11). The total file contains approximately 40 million individual ship reports dating from the mid-19th century. Over 1 million of the reports are within the area of the California Current system.

I have compiled long-term composite monthly fields of surface wind stress on a 1-degree square area basis within the geographical area outlined in Figure 1. The data grid extends from lat. 20°N to 50°N and parallels the coastline configuration, extending 10 degrees of longitude in the offshore direction. Each 1-degree quadrilateral is centered on a whole degree of latitude and longitude. Approximately 25% of the total available reports contain positions recorded to the nearest whole degree of latitude and longitude. The grid orientation used in this study thus minimizes spatial bias which might be introduced by summarizing the data according to the Marsden square numbering system.

The historical data contain errors in position, measurement, and processing. A single pass editor was used to remove gross errors in the data, including duplicate reports (0.5%), position errors (0.1%), and measurement errors (0.5%). Erroneous wind directions and wind speeds greater than 100 m s^{-1} were removed. Reports of variable winds were treated as calms.

An estimate of the surface wind stress was calculated for each wind velocity report according to the bulk formula:

$$(\tau_x, \tau_y) = \rho_a C_D \left(|\vec{W}_{10}| U_{10}, \; |\vec{W}_{10}| V_{10} \right) \qquad (1)$$

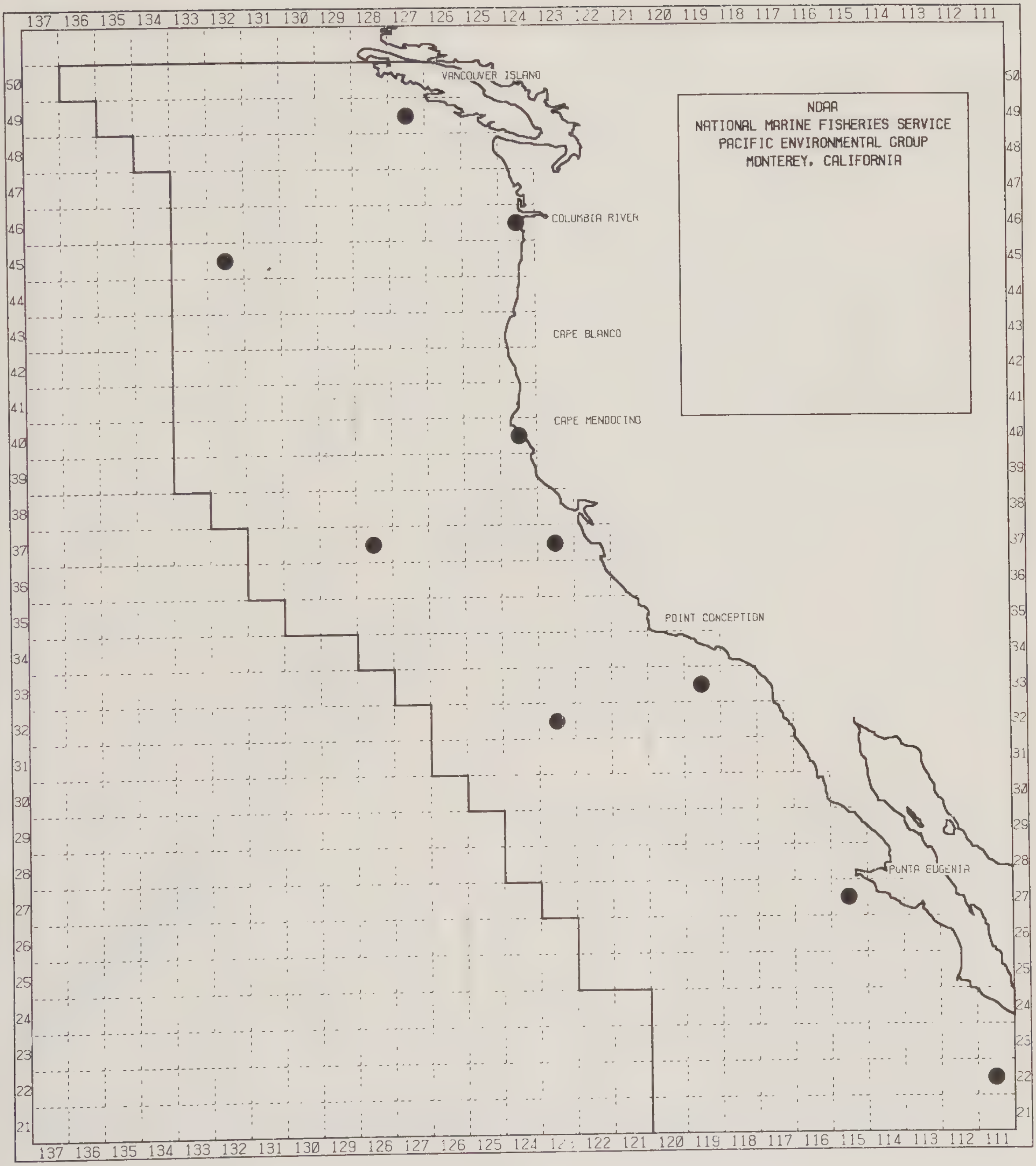
where τ_x and τ_y denote the eastward and northward components of stress, ρ_a is the density of air which was considered to have a constant value of 0.00122 g cm^{-3}, $|\vec{W}_{10}|$ is the observed wind speed, and U_{10} and V_{10} are the eastward and northward components of the wind velocity measured at a height of 10 m. The empirical drag coefficient C_D, referred to the 10-m level, was given a constant value of 0.0013 (Kraus 1972).

The resultant long-term monthly mean wind stress vectors were computed as the arithmetic means by east and north components of all available reports from 1850 to 1972 within a 1-degree square area. The appropriate average is defined in Equation (2):

$$(\bar{\tau}_x, \bar{\tau}_y) = \frac{1}{N} \sum_{i=1}^{N} (\tau_x, \tau_y)_i \qquad (2)$$

where N is the total number of reports within a 1-degree square area and month. The values $(\tau_x, \tau_y)_i$ were evaluated according to Equation (1). A mean value for each long-term month and square is therefore formed from a data set which is independent of all other months and squares. The monthly fields of surface wind stress are displayed in Appendix I as vector quantities (Charts 1 to 12) and as east (Charts 13 to 24) and north (Charts 25 to 36) components. No attempt has been made to smooth the fields, either by removing data which do not appear to fit the distributions or by applying objective smoothing procedures. The mean values were contoured by computer and "bull's-eyes" in the contours, even where they possibly reflect erroneous data, were left in the charts as indications of the general degree of consistency in the composite distributions. The bull's-eyes may reflect either a paucity of ship observations, or extreme variability associated with inadequate sampling of strong winds.

The spatial distribution of observations is biased in that "ship of opportunity" reports are generally confined to coastwise shipping lanes. Contours indicating the total numbers of observations per 1-degree square area are shown in Figure 2. The highest density of reports is found within 300 km of the coast, exceeding 40,000 observations per 1-degree square in the area south of Point Conception. The number of reports per 1-degree square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PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA

Figure 1.—Chart of the west coast of the United States showing the grid of 1-degree squares used for summaries of wind observations. Large dots indicate squares for which frequency diagrams are displayed in Figures 9-12.

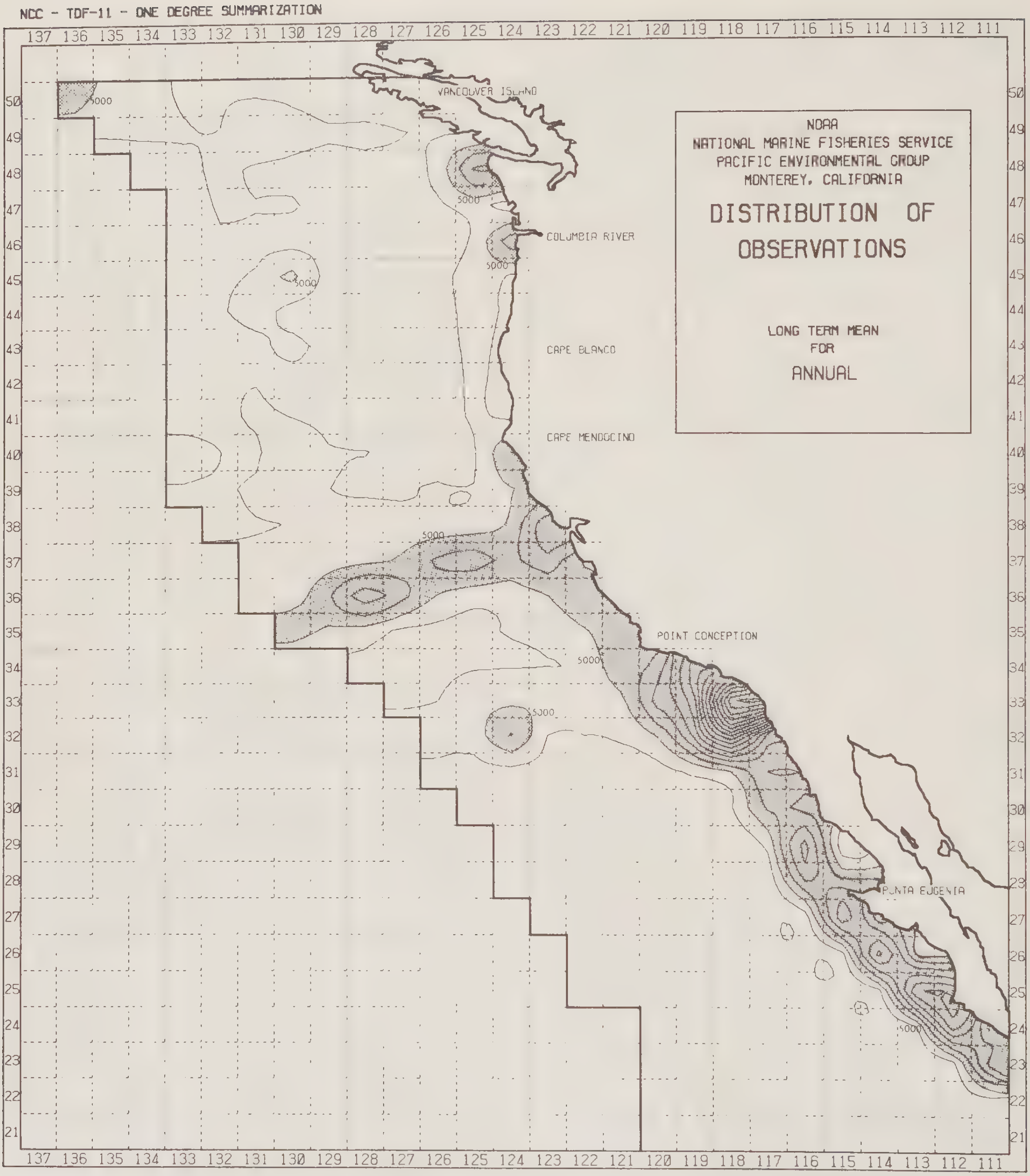
NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
DISTRIBUTION OF OBSERVATIONS
LONG TERM MEAN
FOR
ANNUAL
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
5000

Figure 2.—Distribution of observations per 1-degree square. The contour interval is 2,500 observations. Values greater than 5,000 are shaded.

per month varies from less than 20 (in January off Vancouver Island) to more than 3,800 (in May off Los Angeles). A significant increase in the number of observations is evident along the shipping route between San Francisco and Hawaii. Less than 20% of the vector means are based on fewer than 50 observations per 1-degree square per month. Some temporal bias may also exist, since approximately 50% of the total reports have been taken since 1945. However, the general coherence of the resulting vector fields indicates that the composite wind stress distributions can be used to describe the dominant seasonal cycle in the California Current system.

The historical surface marine observations used in this study have been obtained primarily from ship logs, ship weather reporting forms, and published ship observations. The reports differ markedly in method and precision of measurement, ranging from observations made aboard 19th century vessels, to those taken aboard modern oceanographic research ships. Possible errors in wind measurement have been summarized by Hantel (1970). These include influences of anemometer height, atmospheric stability, wind gusts, and duration of the observation. Sources of error in wind estimates include the wind effects observed, error in determining the true wind from the observed apparent wind, and the unavoidable subjectivity of the observer.

A substantial portion of the historical data consists of wind reports based on the antiquated Beaufort wind force scale (Kinsman 1968). Table 1 lists the conversion scale between the Beaufort number and the equivalent wind speed in knots and meters per second. These estimates are equivalent to a wind speed measurement at a height of 10 m.[2]

Table 1.—Wind speed equivalents of Beaufort force estimates in knots and meters per second.

Beaufort	Knots	ms^{-1}
0	0	0.0
1	2	0.9
2	5	2.4
3	9	4.4
4	13	6.7
5	18	9.3
6	24	12.3
7	30	15.5
8	37	18.9
9	44	22.6
10	52	26.4
11	60	30.5
12	68	34.8

Based on the documentation for the National Climatic Center's data file (TDF-11),[3] a determination was made of the number of wind observations estimated and those actually measured by an anemometer. Approximately 35% of the reports in this study consisted of Beaufort wind force estimates. An additional 53% of the reports were estimated wind speeds which did not correspond to the Beaufort wind force scale. Less than 12% of the total reports consisted of measured quantities.

In addition to the errors introduced by the necessary calculation of true wind from the measured apparent wind, the reported directions varied in precision. Resolution varied from ±11.25° to ±5° corresponding to observations based on 16 points of a 32-point compass and a 36-point compass, respectively.

The above considerations lead to the conclusion that random observational errors may be as large as real nonseasonal fluctuations in the distributions of surface wind stress. The problem may be formalized by expressing the individual stress estimates τ_x and τ_y as the sums of monthly mean values $\bar{\tau}_x$ and $\bar{\tau}_y$, deviations from the monthly means τ'_x and τ'_y, and error terms τ^{ϵ}_x and τ^{ϵ}_y. The second and higher moment statistics will consist of the nonzero correlations between the deviations from the monthly means and the error terms. If the observational errors are greater than the real fluctuations, then the standard deviations of the monthly means will reflect observational noise rather than actual nonseasonal variability. However, provided that these errors are not systematic, the resultant first moment statistics will be the appropriate estimates of the monthly mean wind stress.

The standard error of the mean provides a more appropriate quantitative measure of the relation between the standard deviation of a set of measurements and the precision of the mean value of the data set (Young 1962). The standard errors of the means are defined by:

$$(S_{\bar{\tau}_x}, S_{\bar{\tau}_y}) = (S_{\tau_x}/\sqrt{N}, S_{\tau_y}/\sqrt{N}) \qquad (3)$$

where $S_{\bar{\tau}_x}$ and $S_{\bar{\tau}_y}$ are the standard errors of the means of the eastward and northward components, respectively, S_{τ_x} and S_{τ_y} are the standard deviations, and N is the number of observations. Large values of N and small values of S_{τ_x} and S_{τ_y} correspond to mean values $\bar{\tau}_x$ and $\bar{\tau}_y$ which closely approximate the population means.

The computed standard errors of the means and numbers of observations of each 1-degree square area and long-term month are tabulated in Appendix II. Values less than 0.1 dyne cm^{-2} occur throughout a large portion of the summary area, although spatial and seasonal dependence is evident. Standard errors greater than 0.1 dyne cm^{-2} occur over large areas north of Cape Mendocino and between 500 and 1,000 km off the coast of Baja California. High values are generally associated with regions of sparse date, although inadequate sampling of intense storms may also lead to large values. Typical ratios of the standard error to the mean stress ($S_{\bar{\tau}_x}/\bar{\tau}_x$) range from 0.01 off southern California to 1.0 offshore from Cape Blanco. Near Cape Mendocino, this ratio varies between 0.02 and 0.10. Minimum values adjacent to the coast south of lat. 40°N and along the shipping lane between San Francisco and Hawaii are well correlated with the distribution of observations shown in Figure 2.

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[2] Resolution 9, International Meteorological Committee, Paris, 1946.

[3] National Climatic Center, Tape Data Family 11, NOAA/EDS/NCC, Asheville, N.C.

DEPENDENCE OF STRESS ESTIMATES ON C_D

A constant drag coefficient was used to compute the surface wind stress data displayed in Appendix I. Stress calculations were made for each wind report and then averaged to form the resultant monthly mean vectors. Different results might have been obtained if the stress were calculated from monthly mean wind data, or if effects of atmospheric stability were considered. These aspects are discussed below.

Errors associated with the observational data used in this study place certain limitations on the form of the bulk exchange formula expressed in Equation (1). If measurement errors are large, there may be little value in refining the parameterization by replacing C_D by a variable drag coefficient which is a function of stability or wind speed. Even with a constant C_D, the bulk formula contains nonlinearities. Therefore, the drag coefficient must be appropriate for the particular time-averaged winds used in the calculations. That is, a drag coefficient appropriate for synoptic wind observations would not be appropriate for winds averaged over a month.

Effects of Averaging

The empirically derived transfer coefficient C_D, determined by eddy correlation and profile methods, is based on wind measurements averaged over periods of 30 to 60 min. Pond (1975) indicated that the appropriate values of $|\vec{W}_{10}|$, U_{10}, and V_{10} should be obtained over a period of a few minutes to a few hours at most. If the surface stress were calculated using winds averaged over much longer periods, a higher drag coefficient would be required. The surface stress calculated from a monthly mean surface wind field will be significantly less than the surface stress field calculated as the mean of the individual stress estimates, if the same drag coefficient is used and all other parameters are held constant.

The difference described above has been determined for the data used in this study. For each 1-degree square area and long-term month, the following ratio has been calculated:

$$(C_D)_{\text{equ}} = \overline{|\vec{\tau}|} \Big/ [\rho_a (|\overline{\vec{W}_{10}}|)^2] \qquad (4)$$

where $\overline{|\vec{\tau}|}$ is the magnitude of the monthly mean surface stress, $|\overline{\vec{W}_{10}}|$ is the magnitude of the monthly mean surface wind, and $(C_D)_{\text{equ}}$ is an equivalent drag coefficient. This is the value which would be necessary to make the stress values calculated from the monthly mean wind data agree with the values calculated as the means of individual stress estimates.

Values of $(C_D)_{\text{equ}}$ for the months of June and December are shown in Figures 3 and 4. The values are significantly different from the constant value of $C_D = 0.0013$ employed in this study. In all cases, $(C_D)_{\text{equ}}$ is greater than C_D. Spatial and seasonal variability is marked. There is a tendency for much higher values in the northern section of the grid than in the southern area. Large values of $(C_D)_{\text{equ}}$ are more evident in December than in June. Geographical and seasonal variations in the quantity $(C_D)_{\text{equ}}$ agree with the general geographical and seasonal fluctuations in meteorological conditions over the northeast Pacific Ocean. This would indicate that a large part of the monthly variance of the wind stress data is due to actual intramonth fluctuations and not due to observational errors. If a resultant surface wind stress were calculated from the monthly mean wind field, these calculations imply that the wind stress estimates would be underestimated, on average, by as much as 50% to 100%. The departures would be even larger off Oregon and Washington.

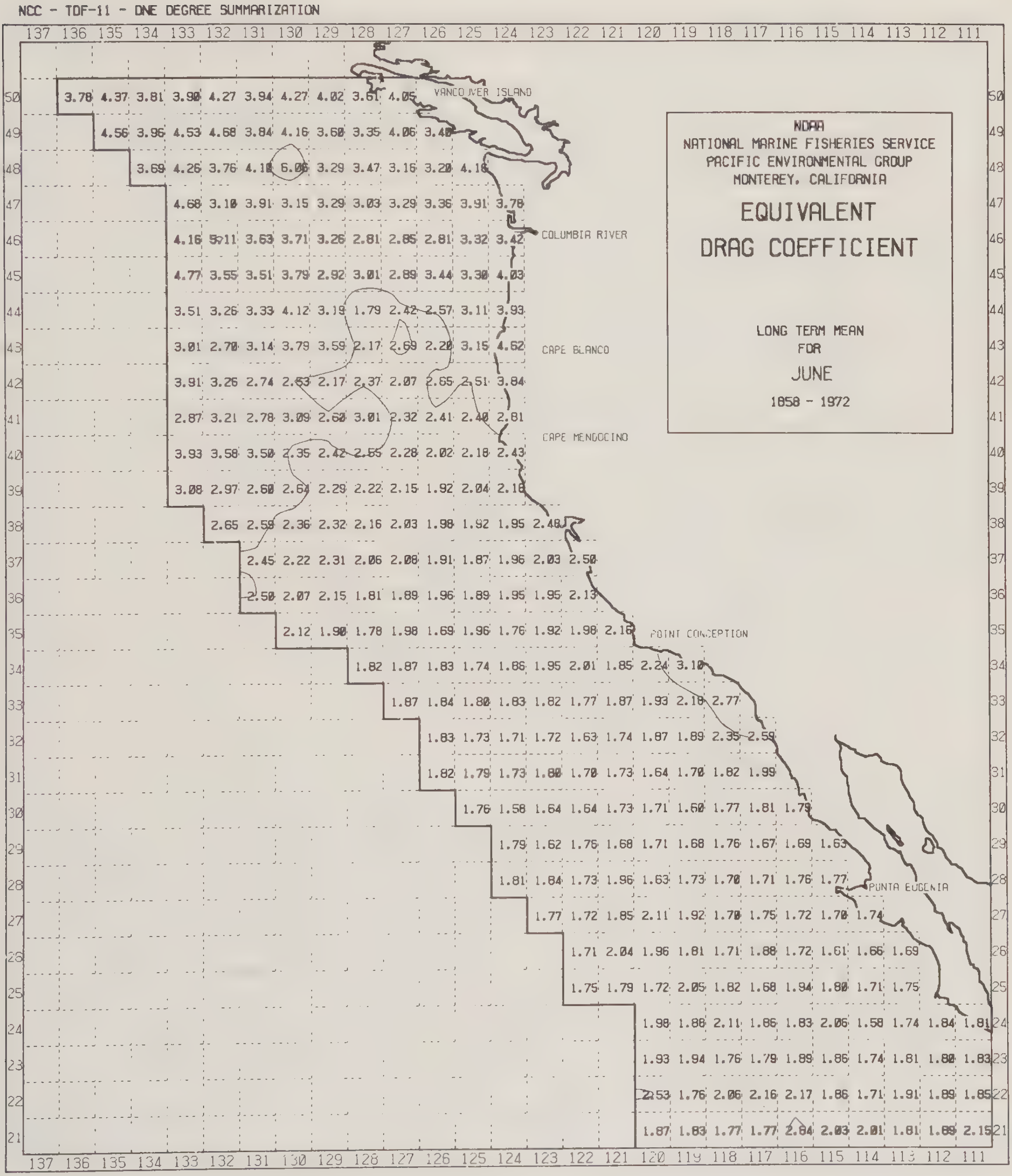
Effect of Atmospheric Stability

Investigations on the functional form of the drag coefficient have alternately suggested constant values, or a dependence on wind speed. Wilson (1960) gave a detailed review of the available data and adopted values of $C_D = 0.0024 \pm 0.005$ for strong winds and $C_D = 0.0015 \pm 0.0008$ for light winds. Smith (1970) proposed a constant value of $C_D = (1.35 \pm 0.34) \times 10^{-3}$. Wu (1969) adopted the form $C_D = (0.5 \times \overline{U}_{10}^{1/2}) \times 10^{-3}$. Considering the large scatter in the open ocean determinations of C_D, the lack of conclusive data at wind speeds greater than 15 ms^{-1}, and the lack of agreement among individual observers, a constant value for the neutral drag coefficient was used in this study.

Recent investigations by Davidson (1974) and Denman and Miyake (1973) have demonstrated the dependence of the drag coefficient on atmospheric stability and the spectral shape of the ocean wave field. A generally accepted formulation of the dependence of C_D on wave properties does not seem well enough established to be incorporated in the calculations of surface wind stress based on historical ship observations. However, effects of atmospheric stability on the momentum exchange may be significant in regions where seasonal upwelling typically produces a stable boundary layer.

The specific effects of atmospheric stability on the exchange of momentum have not been completely determined and are still under investigation. However, for a given wind speed, the effect of stable (unstable) stratification is to decrease (increase) the magnitude of the momentum exchange (surface wind stress) across the atmosphere-ocean interface.

In order to investigate the effects of atmospheric stability, the monthly mean fields of surface wind stress were recomputed, replacing the constant value C_D in Equation (1) by a coefficient varying with atmospheric stability. Deardorff (1968) defined the bulk Richardson number as an appropriate dimensionless measure of atmospheric stability. Deardorff's method was adopted to parameterize the dependence of the drag coefficient on stability, while neutral stability was assumed when the absolute value of the air-sea temperature difference was


NCC - TDF-11 - ONE DEGREE SUMMARIZATION
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PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
EQUIVALENT
DRAG COEFFICIENT
LONG TERM MEAN
FOR
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VANCOUVER ISLAND
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CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
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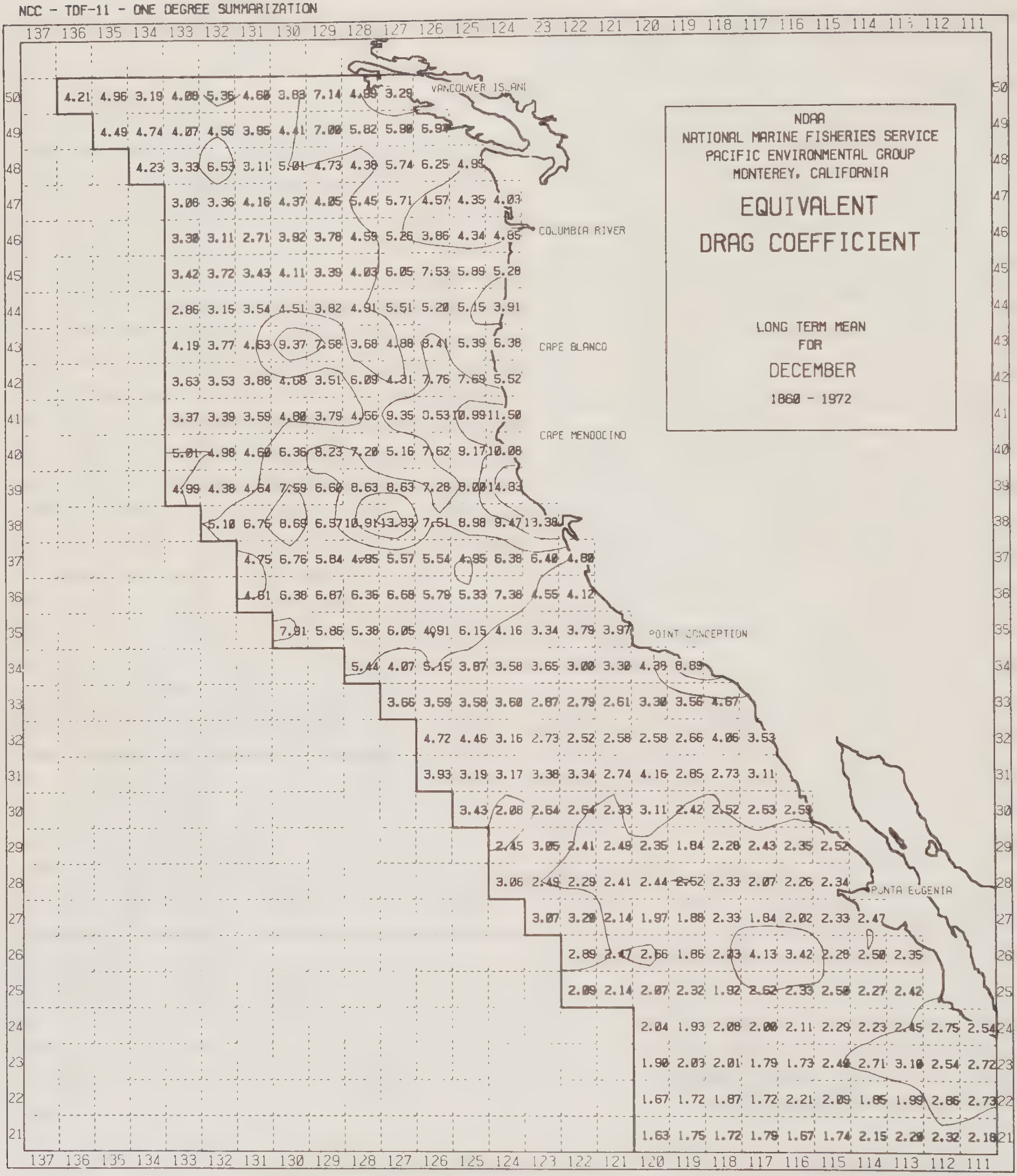
1.87 1.83 1.77 1.77 2.84 2.03 2.01 1.81 1.89 2.15

Figure 3.—Equivalent neutral drag coefficient for June. The plotted value is the drag coefficient ($\times 10^3$) appropriate for wind observations averaged over a month. The contour interval is 2.5.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4.23 3.33 6.53 3.11 5.01 4.73 4.38 5.74 6.25 4.95
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5.10 6.75 8.65 6.57 10.91 13.33 7.51 8.98 9.47 13.38
4.75 6.76 5.84 4.85 5.57 5.54 4.95 6.38 6.40 4.80
4.81 6.38 6.87 6.36 6.68 5.79 5.33 7.38 4.55 4.12
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5.44 4.07 5.15 3.87 3.58 3.65 3.00 3.30 4.38 8.89
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1.90 2.03 2.01 1.79 1.73 2.40 2.71 3.10 2.54 2.72
1.67 1.72 1.87 1.72 2.21 2.09 1.85 1.99 2.86 2.73
1.63 1.75 1.72 1.79 1.67 1.74 2.15 2.20 2.32 2.18

Figure 4.—Equivalent neutral drag coefficient for December. The plotted value is the drag coefficient ($\times 10^3$) appropriate for wind observations averaged over a month. The contour interval is 2.5.

less than 1°C. Details of the calculations will be reported elsewhere.

The effect of atmospheric stability was computed as a percentage increase (decrease) in the magnitude of the monthly mean surface wind stress above (below) the appropriate neutral values. The following ratio was calculated:

$$R = \left(\frac{|\vec{\tau}|_{var}}{|\vec{\tau}|_{neu}} - 1 \right) \times 100 \tag{5}$$

where $|\vec{\tau}|_{var}$ is the magnitude of the monthly mean surface wind stress calculated using a drag coefficient which varies with stability, and $|\vec{\tau}|_{neu}$ is the magnitude of the monthly mean surface wind stress computed with a constant (neutral) coefficient. A value of $R = 0.0$ corresponds to neutrally stable conditions.

The ratio defined by Equation (5) is displayed in Figures 5 and 6 for the months of June and December, respectively. The average percentage difference is between 2 and 5%. Values greater than 10% are rare. In December, the values are positive, indicating unstable conditions. Negative values occur in June. These are related to the stable stratification induced by positive air-sea temperature differences within the coastal upwelling zone. The effects of atmospheric stability determined in this study are less than the values of 6 to 15% reported by Husby and Seckel (1975) for Ocean Weather Station "Victor," but consistent with the values of less than 5% reported by Dorman et al. (1974) for Ocean Weather Station "November."

WIND STRESS DISTRIBUTIONS

The long-term composite monthly mean fields of surface wind stress are displayed in Appendix I as resultant vectors (Charts 1 to 12), east components (Charts 13 to 24), and north components (Charts 25 to 36). These data indicate two characteristic features. The mean stress tends to be directed equatorward along the coast from Cape Mendocino to Baja California throughout the year. Off the coasts of Oregon and Washington, the wind stress exhibits marked seasonal variability in both magnitude and direction.

The distributions of surface wind stress off Baja California have been previously discussed by Bakun and Nelson (1975).[4] They concluded that most of the seasonal variability is in magnitude rather than direction. The mean surface wind stress tends to have an alongshore, equatorward component during all months, implying conditions generally favorable for coastal upwelling throughout the year. This is contrasted with the situation to the north. Off the coasts of Oregon and Washington, patterns of surface wind stress change seasonally. From December to February, the stress impinges on the coast at Cape Blanco, forming the southern boundary of the low pressure system which develops in the Gulf of Alaska during the winter. From May through September, the surface wind stress veers toward the south. The components are directed onshore and equatorward. The months of March-April and October-November appear as transition periods. The surface wind stress is directed primarily onshore off Washington and Oregon during these months.

The most evident feature in these distributions is the position and extent of the predominant wind stress maximum. For purposes of discussion, this maximum is defined by the 1.0 dyne cm^{-2} contour and is highlighted by light shading in Charts 1 to 12. Large values of stress occurring between lat. 45°N and 50°N during winter are probably associated with either high winds or sparse data, and will be ignored in this discussion.

The maximum is first evident in March, south of Point Conception. During succeeding months, the maximum strengthens, increases in size, and shifts northward. In April, values exceeding 1.0 dyne cm^{-2} cover an area from Point Conception to San Francisco. Winds off Oregon have veered, suggesting an alongshore component and implying conditions generally favorable for coastal upwelling. The pattern of surface wind stress is repeated in May. The northern boundary of the central maximum reaches the coast south of Cape Blanco.

The mean wind stress reaches maximum intensity during June and July off Cape Mendocino, where characteristic values exceed 1.5 dynes cm^{-2}. The large-scale maximum extends approximately 500 km in the offshore direction and 1,000 km in the longshore direction. A more intense coastal maximum ($|\vec{\tau}| \geq 1.5$ dynes cm^{-2}) is coherent over an area approximately one-fifth this size. Maximum values of mean surface wind stress typically occur 200 to 300 km off the coast, rather than adjacent to the coast. This feature was previously observed by Munk (1950) and Reid et al. (1958). Mean distributions for August and September suggest relaxing conditions; the maximum is reduced in extent and intensity. These months still exhibit a degree of equatorward stress along the coasts of Oregon and Washington, but in October, the direction backs to the north. The poleward components correspond to onshore Ekman transport and subsequent downwelling at the coast. The distributions for November, December, January, and February indicate characteristic winter conditions. Mean values are typically less than 0.5 dyne cm^{-2}. High winds associated with intense storm activity in the North Pacific Ocean result in regions of mean surface wind stress exceeding 1.0 dyne cm^{-2} off the coasts of Oregon and Washington.

Seasonality of the surface wind stress and its association with coastal upwelling are easily observed along the northern section of the grid. Large changes in mean direction are apparent. Maximum magnitudes occur during the winter. Winds favorable for coastal upwelling occur from April to September. During the remaining months, the direction of the mean surface wind stress corresponds to downwelling at the coast.

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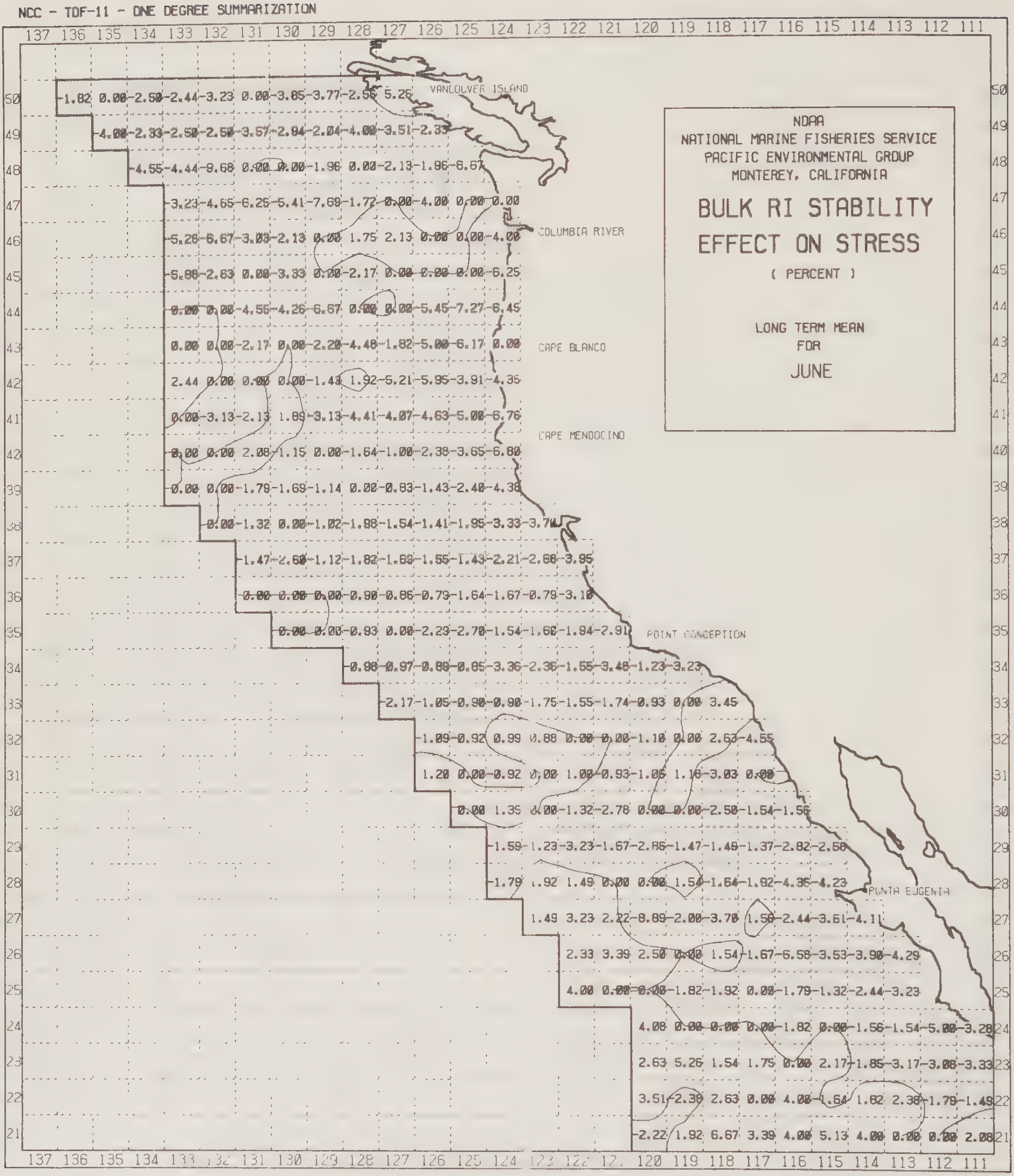
[4] Bakun, A. and C. S. Nelson, 1975. Climatology of upwelling-related processes off Baja California. Unpubl. manuscr., 41 p. On file at Pacific Environmental Group, National Marine Fisheries Service, NOAA, Monterey, CA 93940.



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MONTEREY, CALIFORNIA
BULK RI STABILITY
EFFECT ON STRESS
(PERCENT)
LONG TERM MEAN
FOR
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VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
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-4.00 -2.33 -2.50 -2.50 -3.57 -2.94 -2.04 -4.00 -3.51 -2.33
-4.55 -4.44 -9.68 0.00 0.00 -1.96 0.00 -2.13 -1.96 -6.67
-3.23 -4.65 -6.25 -5.41 -7.69 -1.72 0.00 -4.00 0.00 0.00
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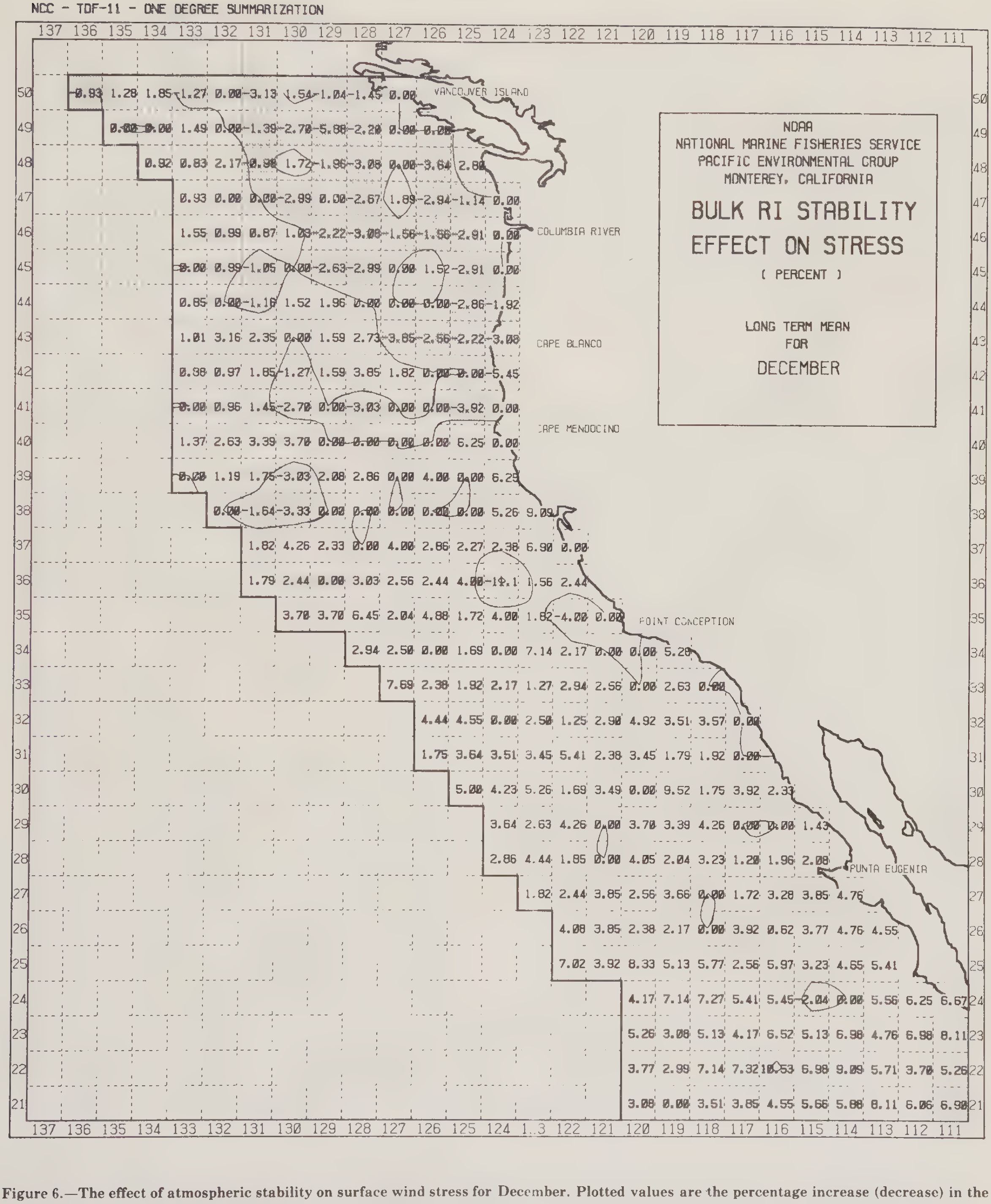
4.00 0.00 0.00 -1.82 -1.92 0.00 -1.79 -1.32 -2.44 -3.23
4.08 0.00 0.00 0.00 -1.82 0.00 -1.56 -1.54 -5.00 -3.28
2.63 5.26 1.54 1.75 0.00 2.17 -1.85 -3.17 -3.08 -3.33
3.51 -2.38 2.63 0.00 4.00 -1.64 1.82 2.38 -1.79 -1.49
-2.22 1.92 6.67 3.39 4.00 5.13 4.00 0.00 0.00 2.08

Figure 5.—The effect of atmospheric stability on surface wind stress for June. Plotted values are the percentage increase (decrease) in the surface wind stress above (below) neutrally stable conditions. The contour interval is 10.0. Positive values correspond to unstable conditions. Negative values are shaded.


NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
BULK RI STABILITY
EFFECT ON STRESS
(PERCENT)
LONG TERM MEAN
FOR
DECEMBER
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
-0.83 1.28 1.85 -1.27 0.00 -3.13 1.54 -1.04 -1.45 0.00
0.00 0.00 1.49 0.00 -1.39 -2.70 -5.88 -2.20 0.00 0.00
0.92 0.83 2.17 -0.98 1.72 -1.96 -3.08 0.00 -3.64 2.80
0.93 0.00 0.00 -2.99 0.00 -2.67 1.89 -2.94 -1.14 0.00
1.55 0.99 0.87 1.03 -2.22 -3.08 -1.56 -1.56 -2.91 0.00
0.00 0.99 -1.05 0.00 -2.63 -2.99 0.00 1.52 -2.91 0.00
0.85 0.00 -1.16 1.52 1.96 0.00 0.00 0.00 -2.86 -1.92
1.01 3.16 2.35 0.00 1.59 2.73 -3.85 -2.56 -2.22 -3.08
0.98 0.97 1.85 -1.27 1.59 3.85 1.82 0.00 0.00 -5.45
0.00 0.96 1.45 -2.70 0.00 -3.03 0.00 0.00 -3.92 0.00
1.37 2.63 3.39 3.70 0.00 0.00 0.00 0.00 6.25 0.00
0.00 1.19 1.75 -3.03 2.08 2.86 0.00 4.00 0.00 6.25
0.00 -1.64 -3.33 0.00 0.00 0.00 0.00 0.00 5.26 9.09
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1.79 2.44 0.00 3.03 2.56 2.44 4.00 -10.1 1.56 2.44
3.70 3.70 6.45 2.04 4.88 1.72 4.00 1.82 -4.00 0.00
2.94 2.50 0.00 1.69 0.00 7.14 2.17 0.00 0.00 5.26
7.69 2.38 1.82 2.17 1.27 2.94 2.56 0.00 2.63 0.00
4.44 4.55 0.00 2.50 1.25 2.90 4.92 3.51 3.57 0.00
1.75 3.64 3.51 3.45 5.41 2.38 3.45 1.79 1.92 0.00
5.00 4.23 5.26 1.69 3.49 0.00 9.52 1.75 3.92 2.33
3.64 2.63 4.26 0.00 3.70 3.39 4.26 0.00 0.00 1.43
2.86 4.44 1.85 0.00 4.05 2.04 3.23 1.20 1.96 2.08
1.82 2.44 3.85 2.56 3.66 0.00 1.72 3.28 3.85 4.76
4.08 3.85 2.38 2.17 0.00 3.92 0.62 3.77 4.76 4.55
7.02 3.92 8.33 5.13 5.77 2.56 5.97 3.23 4.65 5.41
4.17 7.14 7.27 5.41 5.45 -2.04 0.00 5.56 6.25 6.67
5.26 3.08 5.13 4.17 6.52 5.13 6.98 4.76 6.98 8.11
3.77 2.99 7.14 7.32 10.53 6.98 9.09 5.71 3.70 5.26
3.08 0.00 3.51 3.85 4.55 5.66 5.88 8.11 6.06 6.90

Figure 6.—The effect of atmospheric stability on surface wind stress for December. Plotted values are the percentage increase (decrease) in the surface wind stress above (below) neutrally stable conditions. The contour interval is 10.0. Positive values correspond to unstable conditions. Negative values are shaded.

The coast along southern California and Baja California is characterized by winds favorable for upwelling throughout the year. Peak values of surface wind stress occur in April and May. Values exceeding 0.5 dyne cm^{-2} are evident from February to July. A local maximum immediately north of Punta Eugenia is easily observed in May. This feature is consistent throughout the year. A region of local wind stress minima is indicated along the coast south of Point Conception. This feature corresponds in location with the semipermanent cyclonic eddy which dominates the ocean surface circulation in the Southern California Bight (Reid et al. 1958).

Spatial and Temporal Variability

Spatial and seasonal variability of the monthly distributions will be described in terms of standard errors of the means (Equation (3)), constancy of the wind stress, and frequency diagrams for selected 1-degree square areas and months. In general, these data indicate greater variability in magnitude and direction in the region north of Cape Mendocino than in the area to the south. Summer distributions are characterized by well-defined mean directions and magnitudes. Broad-banded frequency histograms are typical of winter months.

The degree of variability in direction and magnitude of the surface wind stress is reflected in the spatial distributions of the standard errors of the means. In regions outside of the primary shipping lanes (see Fig. 2), monthly mean distributions are based on approximately the same number of observations per 1 degree square area. If one assumes that there are no systematic sampling errors in these regions, then the magnitudes of the computed standard errors of the means should be a function of the wind stress variability. Accordingly, standard errors to the north of Cape Mendocino are larger by a factor of 2 to 3 (Appendix II) than those to the south of Cape Mendocino. Thus, the data imply a greater degree of variation in the direction and magnitude of the surface wind stress off Oregon and Washington than off California.

A contrast between winter and summer conditions is also evident. South of Cape Mendocino, magnitudes of the standard errors of the means remain nearly constant throughout the year. Off Oregon and Washington, the computed values decrease to a minimum during the summer, and increase to a maximum during the winter. Typical values range from 0.10 dyne cm^{-2} in June to 0.30 dyne cm^{-2} in December.

Similar features of the large-scale temporal and spatial variations are evident in monthly distributions of constancy of the wind stress as defined by the ratio of the magnitude of the average stress to the average magnitude of the stress. Figures 7 and 8 show the patterns for June and December. During December, values greater than 0.5 occur south of Point Conception. To the north, wind stress constancy decreases to relatively small values, implying a high degree of directional variability. An increase in directional constancy is indicated during June. Values greater than 0.50 extend from Baja California to Vancouver Island. Values less than 0.50 occur only in the northwest section of the grid. South of Cape Mendocino, the ratios approach a value of 1.0, implying very little variation in wind stress direction.

The patterns of wind stress constancy indicate possible error in estimates of the total mechnical energy transfer at the air-sea interface. In the region off California, the magnitude of the mean vector wind stress appears to be a good estimator of the total stress acting on the sea surface. However, in the northern regions of the data grid, these data show that the magnitude of the mean vector wind stress underestimates the total stress acting on the sea surface. This has important implications for mixed-layer modelling, in which the input of turbulent energy depends on the total stress acting on the sea surface (Denman 1973), the direction of the surface stress, and the rate at which the stress is applied to the sea surface (Niiler 1975).

The large-scale spatial and temporal variations in surface wind stress distributions are finally described in terms of selected frequency diagrams. Data for the 10 squares indicated in Figure 1 are displayed in Figures 9 to 12. Figures 9 and 10 show data for June and December taken from the five squares indicated in the inset. Similar data at five different locations are presented for July and January in Figures 11 and 12.[5]

Available wind stress data have been classed by direction and magnitude for each 1-degree square area and month. Relative frequencies have been determined for 16 direction bands and for 11 magnitude bands. A category for calm winds also includes variable winds. The direction bands are 22.5° wide and the magnitude bands correspond to equivalent wind speed intervals of 2.0 m s^{-1}.

The relative frequency surfaces shown in these figures display contours of percentage of total reports falling within a given direction and magnitude band. The 2.5% and 7.5% contours are indicated by a solid line. Dashed line contours indicate relative frequencies of 5.0% and 10.0%. The mean vector magnitude and direction is indicated by an arrow. Note that directions are defined with the oceanographic convention (i.e., the direction toward which the wind blows).

The histograms shown to the right of each frequency surface display relative frequencies for magnitude at the top, and direction at the bottom. Relative percent is labelled along the ordinate. Midpoints of the magnitude and direction class intervals are labelled on the abscissa.

The contrast between winter and summer distributions in the southern section of the grid appears as a change in the character of the frequency surfaces (Figs. 9, 10). In general, the number of contours indicated for June is greater than the number of contours appearing in December. Evidently, the wind stress is relatively constant in magnitude and direction during the summer

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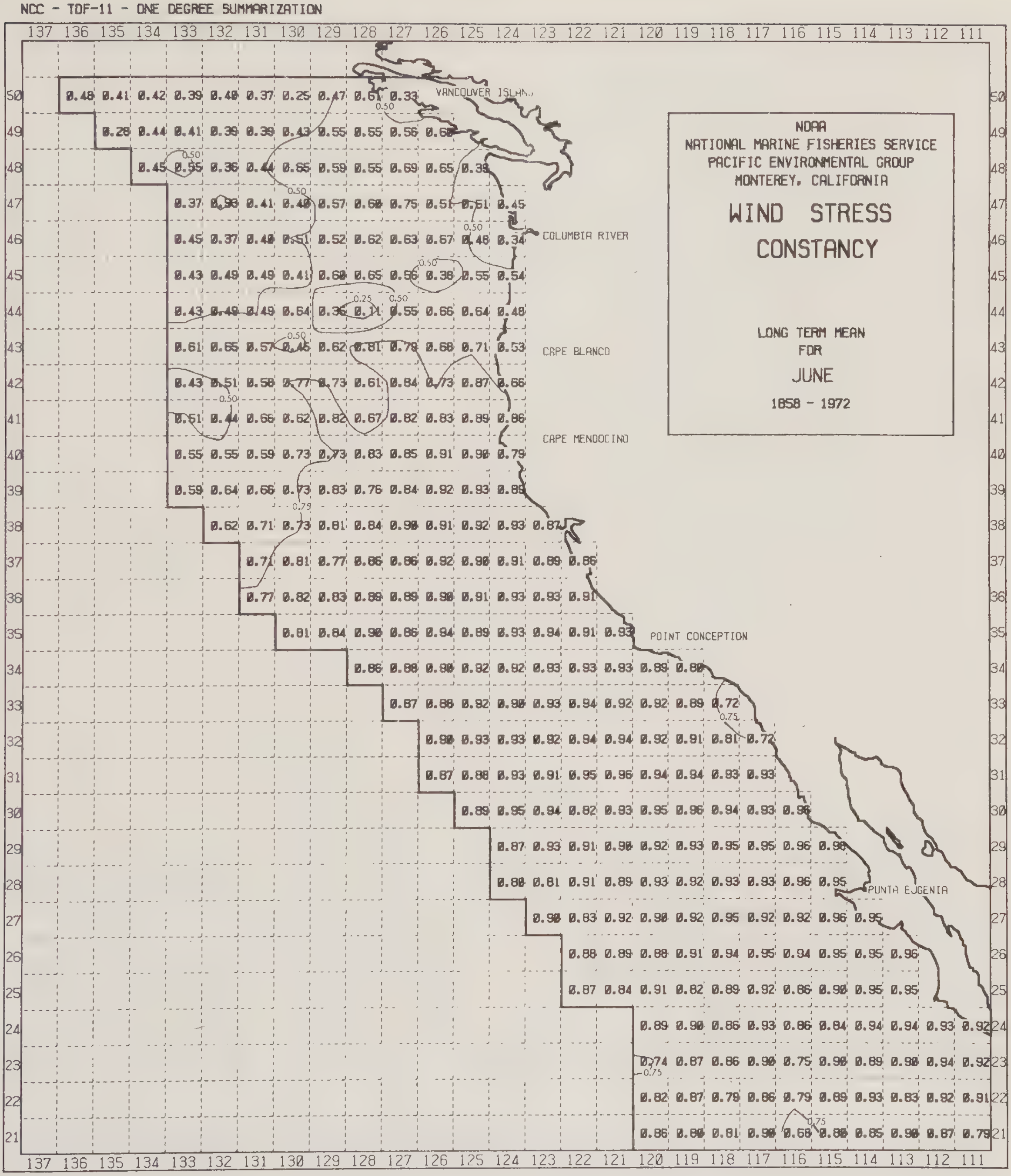
[5] Wind roses for all 1-degree squares within the area north of lat. 34°N may be found in *Climatic study of the near coastal zone; West Coast of the United States*, published by the Director, Naval Oceanography and Meteorology, June 1976, 133 p.


NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
WIND STRESS CONSTANCY
LONG TERM MEAN FOR
JUNE
1858 - 1972
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
50 0.48 0.41 0.42 0.39 0.40 0.37 0.25 0.47 0.61 0.33
49 0.28 0.44 0.41 0.39 0.39 0.43 0.55 0.55 0.56 0.60
48 0.45 0.55 0.36 0.44 0.65 0.59 0.55 0.69 0.65 0.39
47 0.37 0.38 0.41 0.40 0.57 0.60 0.75 0.51 0.51 0.45
46 0.45 0.37 0.40 0.51 0.52 0.62 0.63 0.67 0.46 0.34
45 0.43 0.49 0.49 0.41 0.60 0.65 0.56 0.38 0.55 0.54
44 0.43 0.49 0.49 0.64 0.36 0.11 0.55 0.66 0.64 0.48
43 0.61 0.65 0.57 0.45 0.62 0.81 0.78 0.68 0.71 0.53
42 0.43 0.51 0.58 0.77 0.73 0.61 0.84 0.73 0.87 0.66
41 0.51 0.44 0.66 0.62 0.82 0.67 0.82 0.83 0.89 0.86
40 0.55 0.55 0.59 0.73 0.73 0.83 0.85 0.91 0.90 0.79
39 0.59 0.64 0.66 0.73 0.83 0.76 0.84 0.92 0.93 0.89
38 0.62 0.71 0.73 0.81 0.84 0.90 0.91 0.92 0.93 0.87
37 0.71 0.81 0.77 0.86 0.86 0.92 0.90 0.91 0.89 0.86
36 0.77 0.82 0.83 0.89 0.89 0.90 0.91 0.93 0.93 0.91
35 0.81 0.84 0.90 0.86 0.94 0.89 0.93 0.94 0.91 0.93
34 0.86 0.88 0.90 0.92 0.92 0.93 0.93 0.93 0.89 0.80
33 0.87 0.88 0.92 0.90 0.93 0.94 0.92 0.92 0.89 0.72
32 0.90 0.93 0.93 0.92 0.94 0.94 0.92 0.91 0.81 0.72
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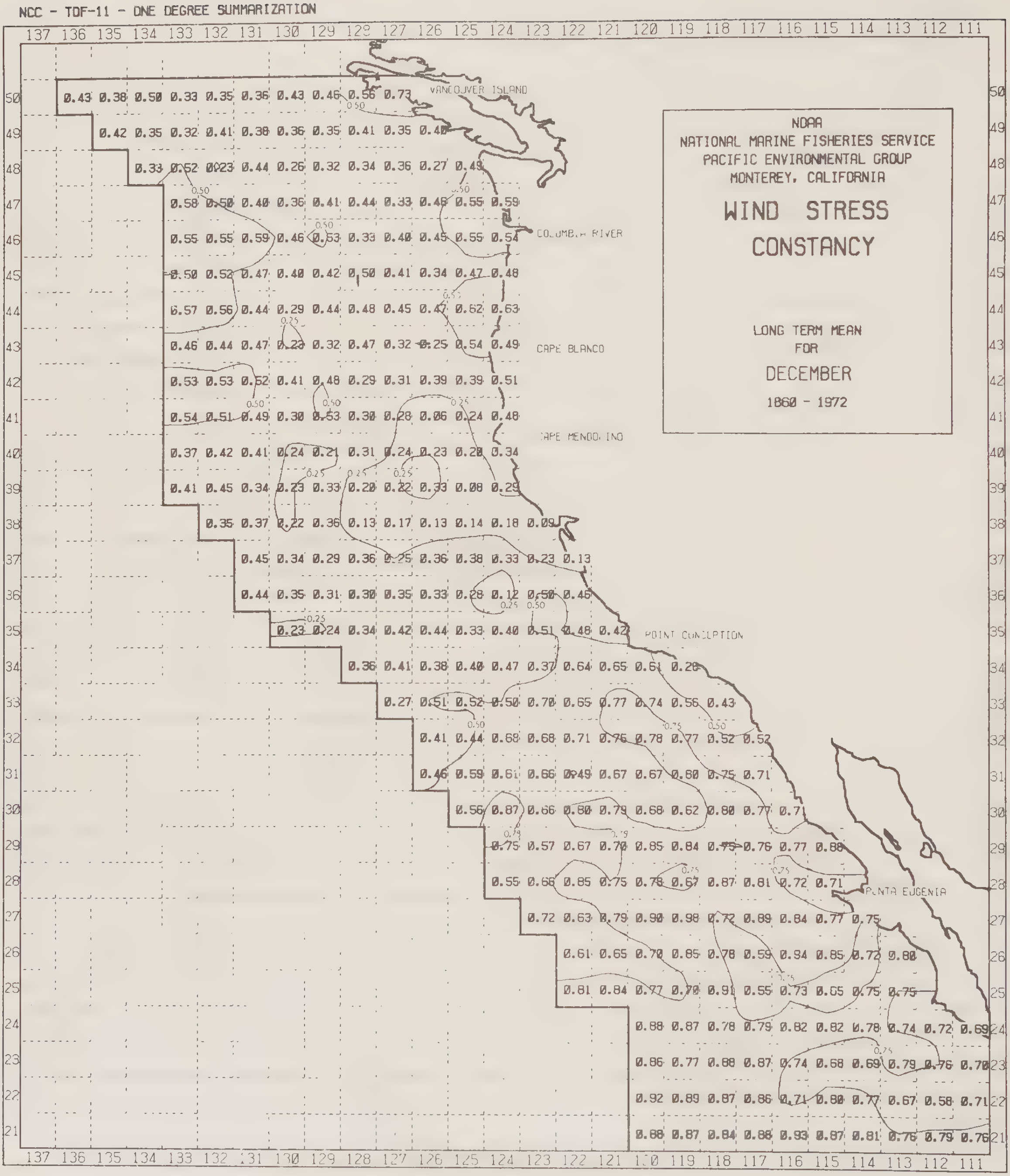
23 0.74 0.87 0.86 0.90 0.75 0.90 0.89 0.90 0.94 0.92
22 0.82 0.87 0.79 0.86 0.79 0.89 0.93 0.83 0.92 0.91
21 0.86 0.80 0.81 0.90 0.68 0.80 0.85 0.90 0.87 0.79
0.50
0.25
0.75

Figure 7.—Wind stress constancy for June. The plotted values are defined as the ratios of the vector means to the scalar means. The contour interval is 0.25.


NCC - TDF-11 - ONE DEGREE SUMMARIZATION
NOAA
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MONTEREY, CALIFORNIA
WIND STRESS
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137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
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0.50 0.52 0.47 0.40 0.42 0.50 0.41 0.34 0.47 0.48
0.57 0.56 0.44 0.29 0.44 0.48 0.45 0.47 0.62 0.63
0.46 0.44 0.47 0.23 0.32 0.47 0.32 0.25 0.54 0.49
0.53 0.53 0.52 0.41 0.48 0.29 0.31 0.39 0.39 0.51
0.54 0.51 0.49 0.30 0.53 0.30 0.28 0.06 0.24 0.48
0.37 0.42 0.41 0.24 0.21 0.31 0.24 0.23 0.20 0.34
0.41 0.45 0.34 0.23 0.33 0.20 0.22 0.33 0.08 0.29
0.35 0.37 0.22 0.36 0.13 0.17 0.13 0.14 0.18 0.09
0.45 0.34 0.29 0.36 0.25 0.36 0.38 0.33 0.23 0.13
0.44 0.35 0.31 0.30 0.35 0.33 0.28 0.12 0.50 0.45
0.23 0.24 0.34 0.42 0.44 0.33 0.40 0.51 0.48 0.42
0.36 0.41 0.38 0.40 0.47 0.37 0.64 0.65 0.61 0.28
0.27 0.51 0.52 0.50 0.70 0.65 0.77 0.74 0.56 0.43
0.41 0.44 0.68 0.68 0.71 0.76 0.78 0.77 0.52 0.52
0.46 0.59 0.61 0.66 0.49 0.67 0.67 0.80 0.75 0.71
0.56 0.87 0.66 0.80 0.79 0.68 0.62 0.80 0.77 0.71
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0.92 0.89 0.87 0.86 0.71 0.80 0.77 0.67 0.58 0.71
0.88 0.87 0.84 0.88 0.93 0.87 0.81 0.76 0.79 0.76

Figure 8.—Wind stress constancy for December. The plotted values are defined as the ratios of the vector means to the scalar means. The contour interval is 0.25.

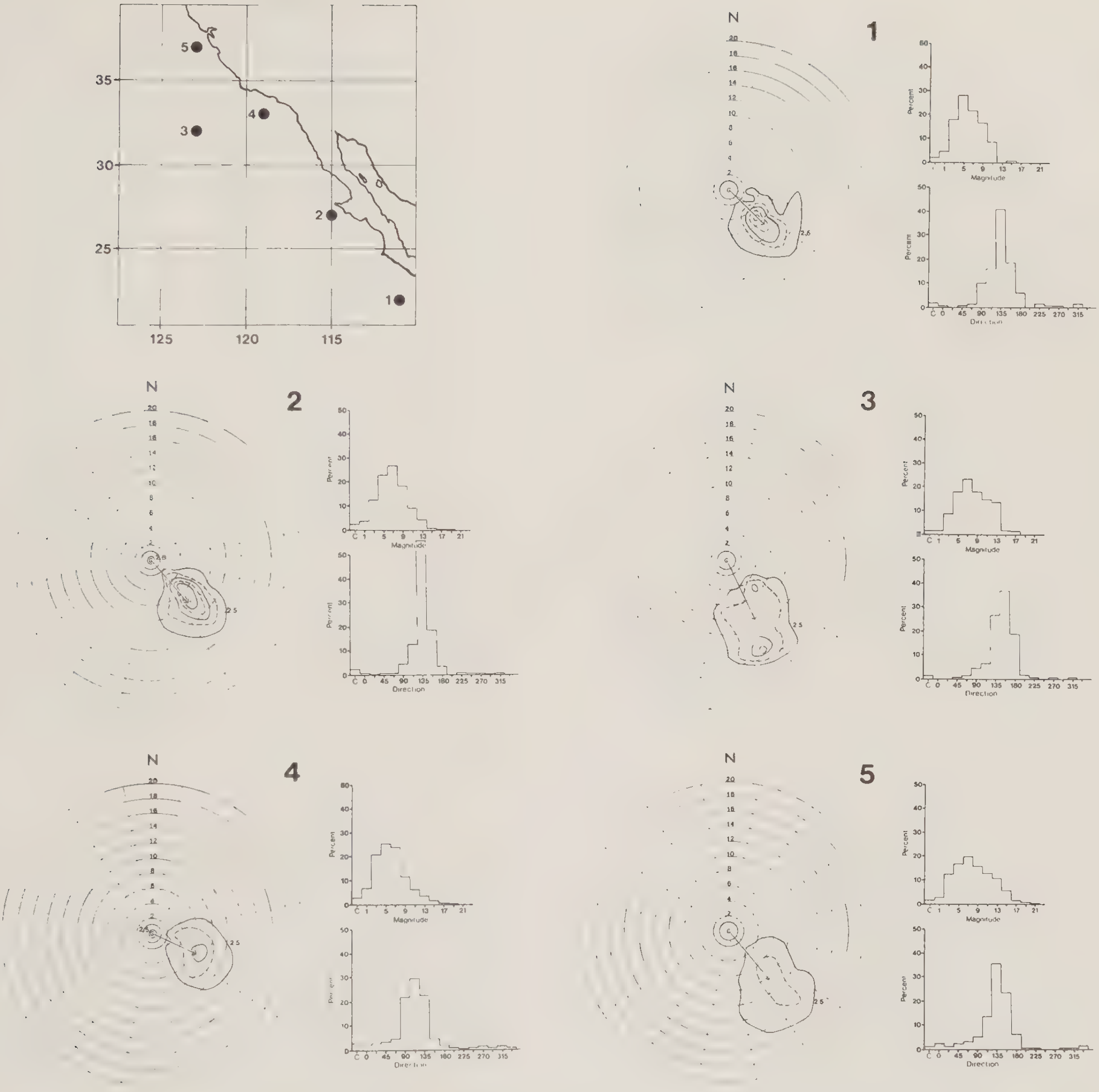


Figure 9.—Relative frequency surfaces and frequency histograms for June. Data are shown for the 1-degree squares labelled 1 through 5 in the upper left inset. Contours of relative frequency are drawn at intervals of 2.5%. Mean vector wind stress is indicated by an arrow.

months. A slight shift in direction and magnitude of the wind stress is indicated between summer and winter. The mean stress in December is directed more toward the south, and the magnitude has decreased.

The frequency histograms also show these features. During June, the direction histogram is characteristically narrow-banded. Over 70% of the observations may be concentrated within three direction intervals. In December, the observations tend to be spread over a wider range of directions. The histograms are broader and the peaks in direction are less well-defined. Peak magnitudes in June are generally one class interval larger than peak magnitudes in December. However, the winter distributions are characterized by an increase in relative frequency at high values of wind stress magnitude.

A similar pattern of contrasts between summer and winter distributions is apparent in the northern section of the grid. As shown in Figures 11 and 12, the direction histograms are generally well-defined during the summer, although bimodal distributions are evident. During winter, observations are nearly uniformly spread among all directions. There is a lack of consistency in the frequency surfaces in Figure 12. Direction histograms for

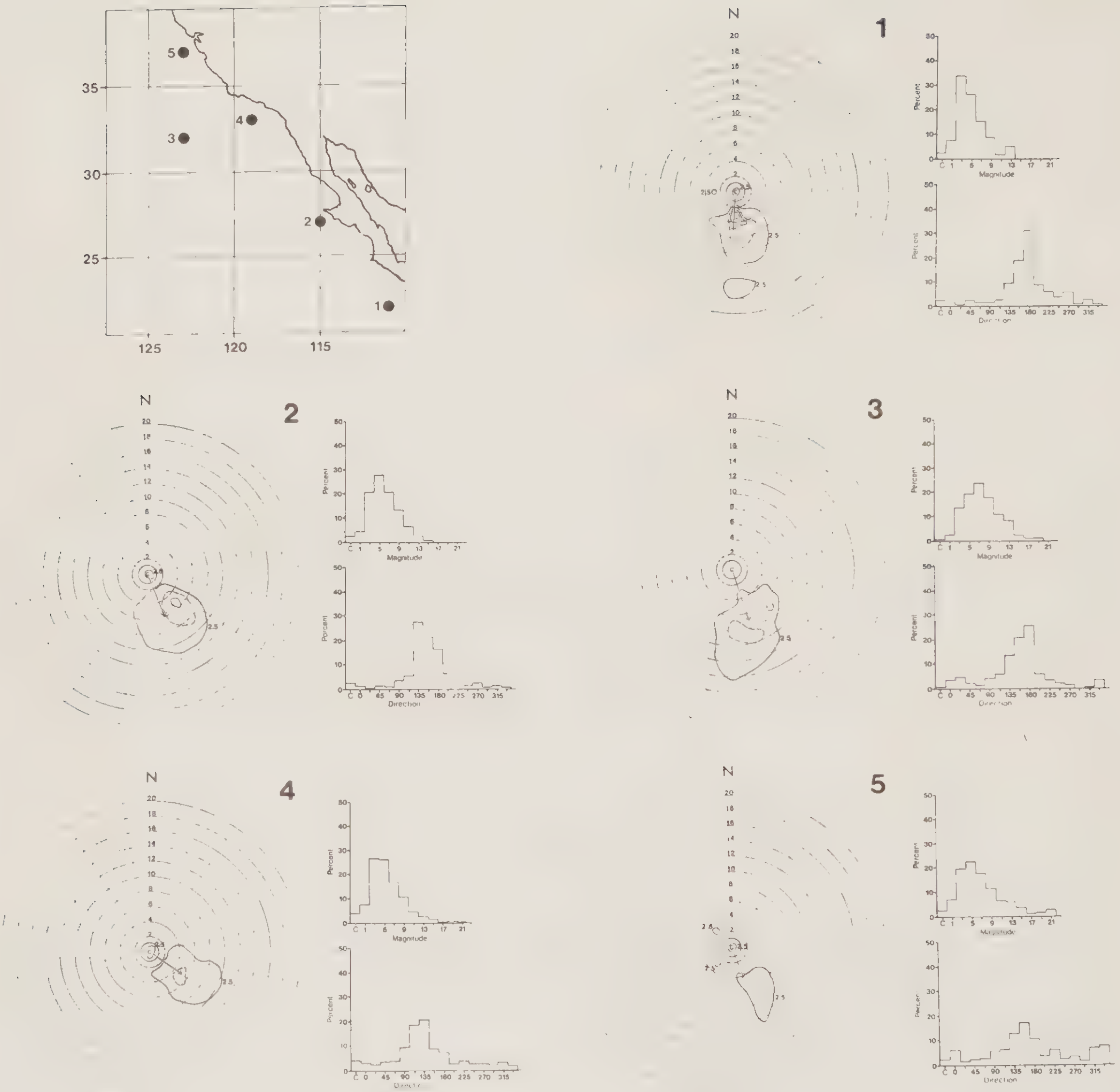


Figure 10.—Relative frequency surfaces and frequency histograms for December. Data are shown for the 1-degree squares labelled 1 through 5 in the upper left inset. Contours of relative frequency are drawn at intervals of 2.5%. Mean vector wind stress is indicated by an arrow.

January are broad and flat and the peaks which generally characterize the summer distributions are missing. Mean directions shift from equatorward to poleward between summer and winter. A complete reversal in the mean direction occurs at point 7 (Figs. 11, 12). A shift in magnitude is equally pronounced. Peak magnitudes are higher in January than in July indicating a greater contribution of high wind speeds in January.

The above discussion adds a new dimension to the seasonal descriptions of the surface wind stress distributions over the California Current. Pronounced seasonal variations in magnitude and direction of the monthly mean wind stress are indicated along the entire west coast of the United States. These changes are most evident off the coasts of Oregon and Washington. In addition, these data suggest month to month changes in the large-scale spatial variability. Frequency histograms for direction and magnitude are broad and flat during the winter months, and along the northern coast. Well-defined peaks in magnitude and direction characterize the distributions during the summer and along the southern coast.

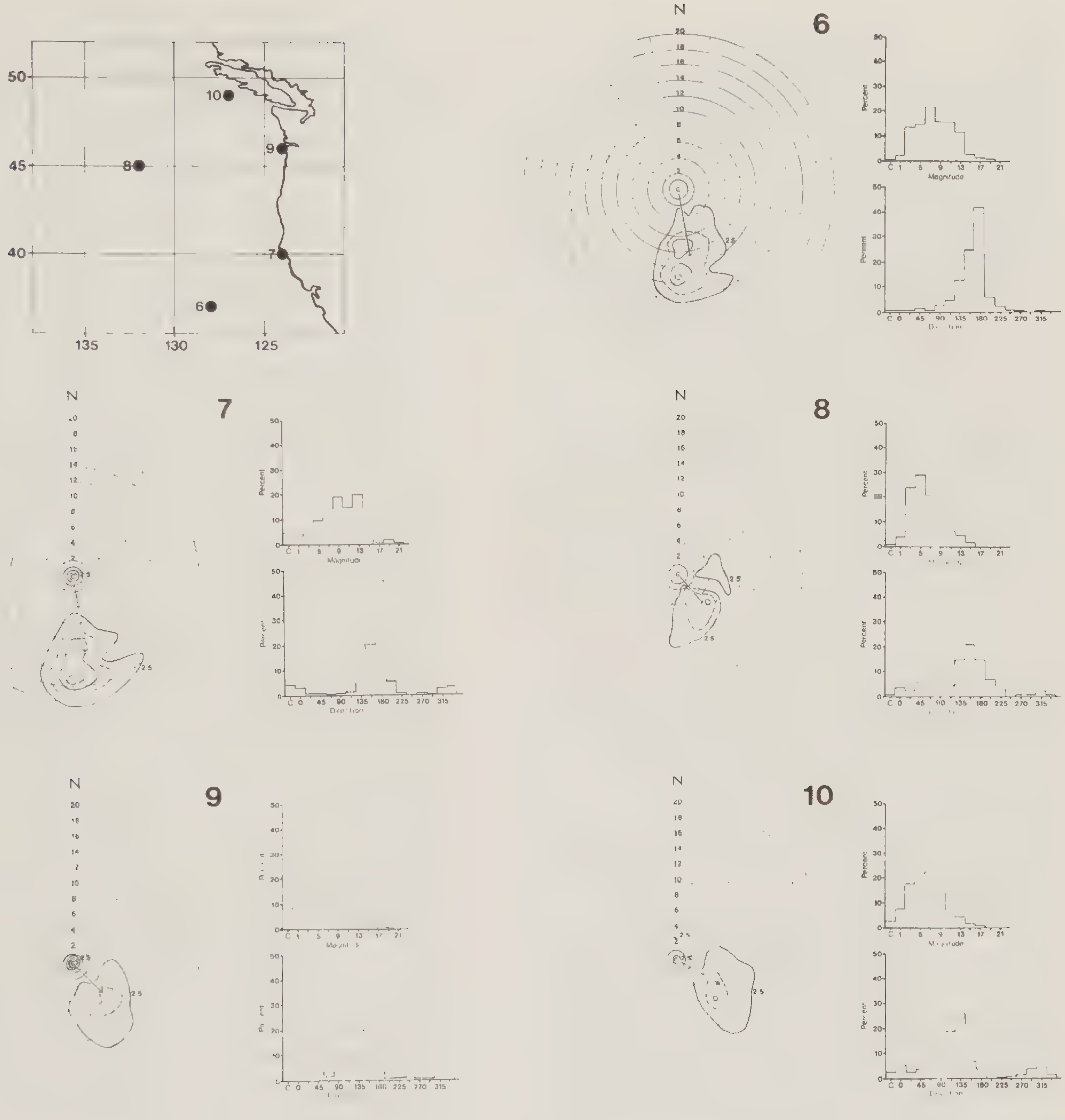


Figure 11.—Relative frequency surfaces and frequency histograms for July. Data are shown for the 1-degree squares labelled 6 through 10 in the upper left inset. Contours of relative frequency are drawn at intervals of 2.5%. Mean vector wind stress is indicated by an arrow.

Seasonal Cycle at the Coast

Time series of the surface wind stress within the 1-degree square areas immediately adjacent to the coast are displayed in Figure 13 as the alongshore component, and in Figure 14 as the onshore component. For these displays, the vector means have been resolved into components parallel and perpendicular to the coast. The coastline angles were determined by visually fitting a line to the dominant trend of the coast within each 1-degree square. The months are indicated along the tops of the figures. The latitudes of the 1-degree squares are indicated on the right and left sides of the figures. Negative values are shaded and indicate equatorward alongshore stress in Figure 13 and offshore stress in Figure 14.

Several characteristic features are apparent in these figures. South of lat. 40°N there is an equatorward component throughout the year, implying conditions favorable for coastal upwelling in all months. Off the coasts of Oregon and Washington, the data suggest that upwelling occurs seasonally between the months of April and September.

Three relative maxima occur in the time/space domain. Off the coast of Baja California, maximum values

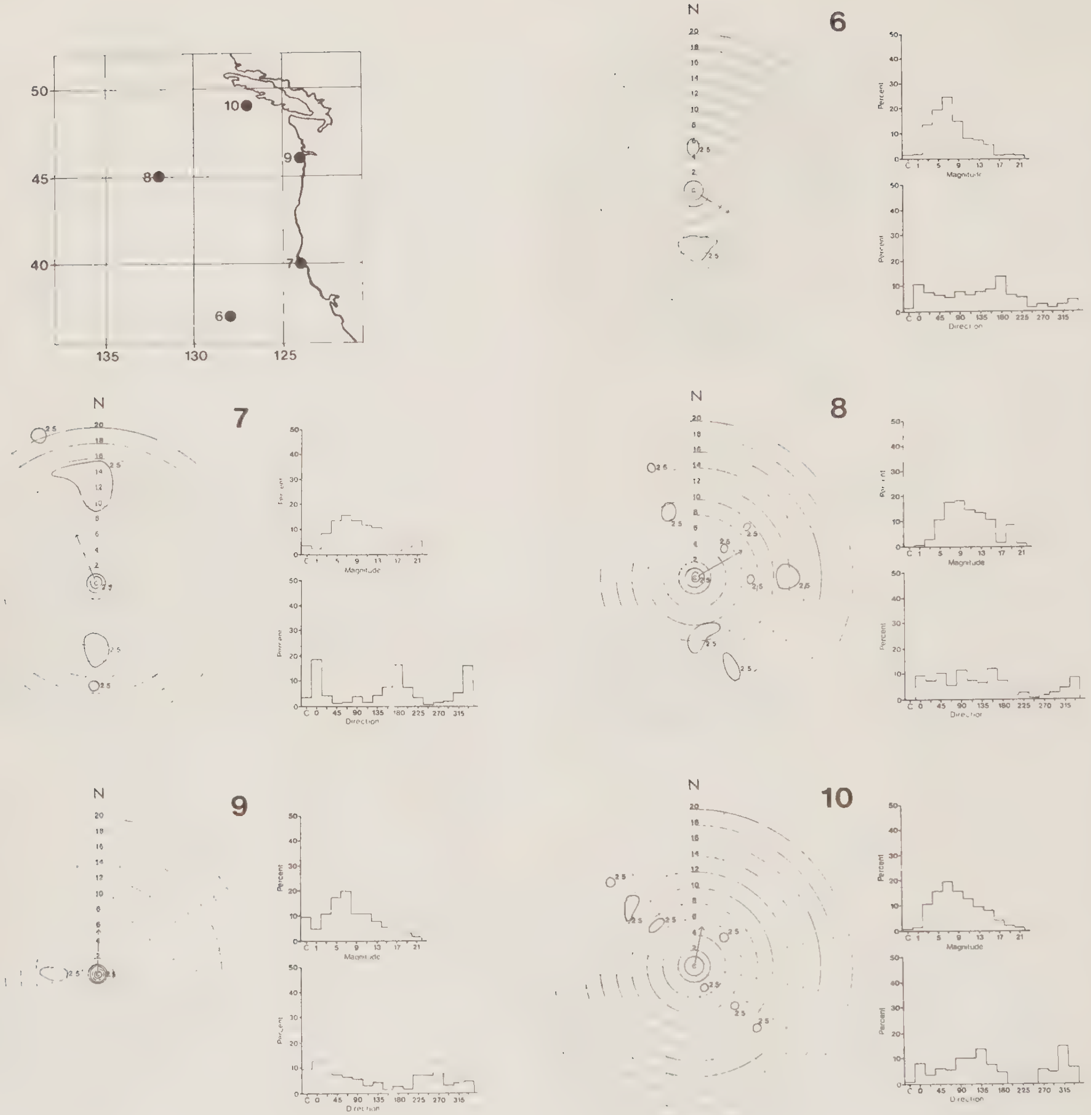


Figure 12.—Relative frequency surfaces and frequency histograms for January. Data are shown for the 1-degree squares labelled 6 through 10 in the upper left inset. Contours of relative frequency are drawn at intervals of 2.5%. Mean vector wind stress is indicated by an arrow.

of wind stress are evident near Punta Eugenia in May. A large maximum occurs just south of Cape Mendocino between May and August. A smaller, local maximum occurs in May and June at lat. 36°N.

Figure 13 is similar in appearance to a time series of offshore Ekman transport shown by Bakun et al. (1974). They showed a good correlation between the occurrence of maximum offshore transport at lat. 39°N and a suppression of seasonal warming in the adjacent coastal waters during early summer, which is indicative of upwelling. The timing of the central wind stress maximum off the coast from Cape Mendocino agrees with the description of the mean yearly cycle of indicated upwelling given by Bakun (1973). However, Bakun's data are spatially distorted, and indicate maximum values at lat. 33°N, long. 119°W in the middle of the Southern California Bight. The spatial distortion is primarily caused by development of an intense thermal low over southern California during the summer. The influence of this low pressure system, and the effects of coastal mountain ranges distort the analyzed pressure fields used in Bakun's computations.

The time series of alongshore surface wind stress (Fig. 13) suggests a slight tilt, with time and space, to the region of maximum values. This corresponds to a northward shift in the intensity of the surface wind stress from

April and May off the coast of Baja California to June, July, and August off Cape Mendocino and Cape Blanco.

Figure 14 indicates a tendency for the surface wind stress to be directed onshore throughout the year north of lat. 30°N. Off the coast of Baja California, surface stress is characterized by offshore components, except between the months of April and October. Offshore components are also apparent in the vicinity of Cape Mendocino and Point Conception. Near these points, abrupt changes in coastline orientation may influence the direction and magnitude of the surface wind stress.

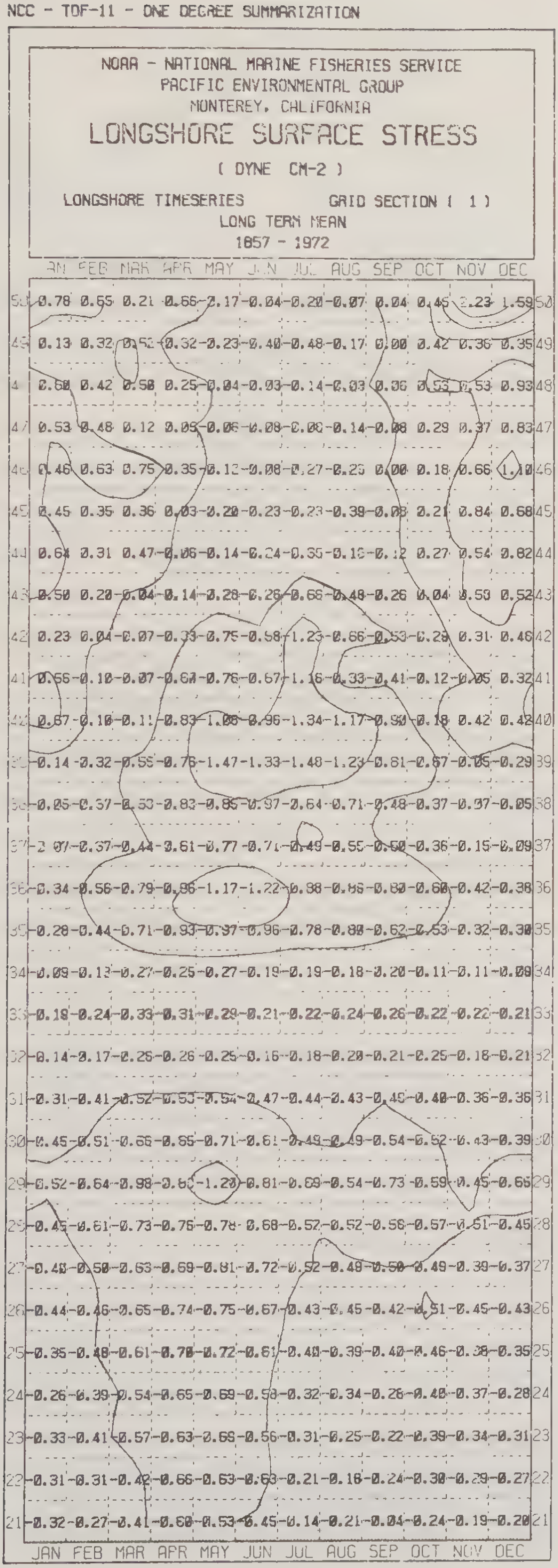
WIND STRESS CURL

The surface wind stress curl is the forcing function for the vertically integrated mass transport of the wind-driven ocean circulation. Under linear, steady-state conditions on the "β-plane," in the absence of friction and interactions with bottom topography, the meridional component of mass transport (M_y) is directly proportional to the vertical component of the curl of the wind stress as expressed in Equation (6):

$$M_y = \frac{\vec{k}\cdot(\nabla\times\vec{\tau})}{\beta} \tag{6}$$

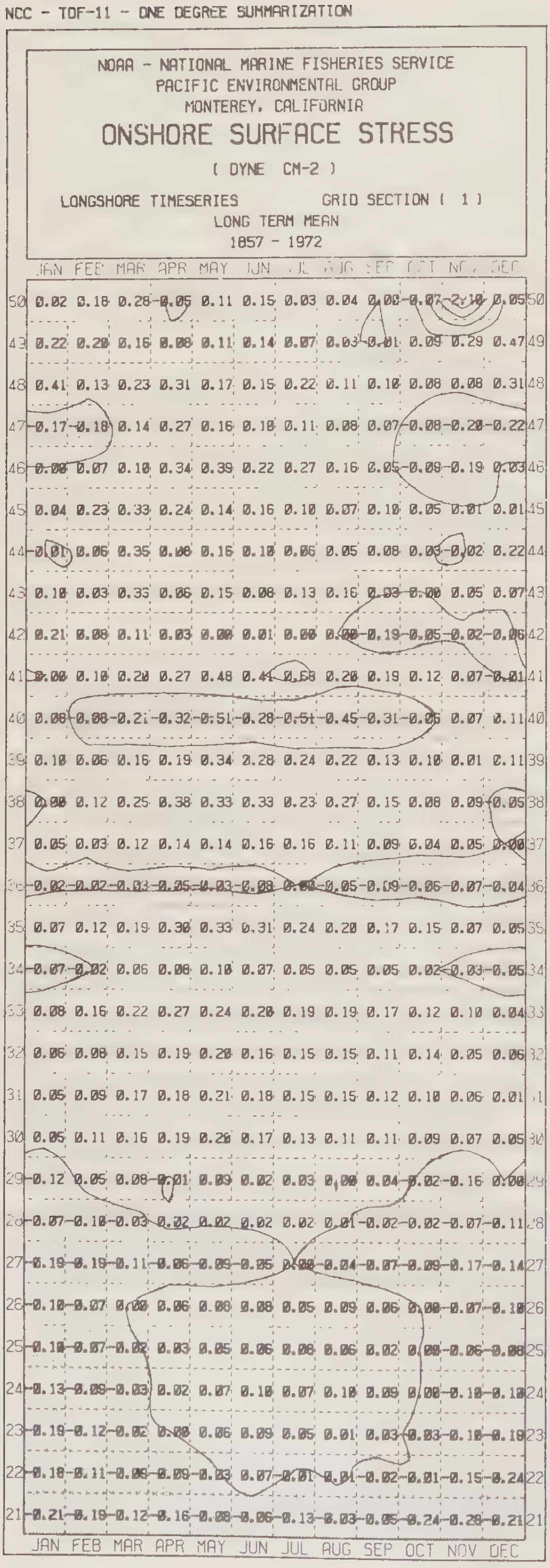
where M_y is the meridional component of the vertically integrated mass transport, β is the meridional derivative of the Coriolis parameter f, and $\vec{k}\cdot(\nabla\times\vec{\tau})$ is the vertical component of the wind stress curl. According to the simplified model, positive (negative) wind stress curl is associated with northward (southward) meridional transport. Surface Ekman divergence (convergence) corresponding to positive (negative) wind stress curl is balanced by geostrophic convergence (divergence) in the northward (southward) meridional flow.

Coastal upwelling occurs only at the ocean boundary. However, wind induced upwelling will occur whenever divergence in the surface wind drift is not balanced by other modes of horizontal surface flow. Figure 15 shows a mechanism by which the wind stress curl determines the divergent or convergent nature of the surface wind drift offshore of the primary coastal upwelling zone. A seaward increase in the equatorward wind stress parallel to the coast (Fig. 15A) is characterized by positive wind stress curl. In this situation, the offshore component of Ekman transport increases in the offshore direction, resulting in continued surface divergence. Upwelling is required to maintain the mass balance. If the equatorward longshore surface wind stress decreases in the offshore direction (Fig. 15B), the wind stress curl is negative. Convergence in the surface wind drift will result. Frontal formation and downwelling may occur just offshore of the primary coastal upwelling zone.



	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	
50	0.78	0.55	0.21	0.66	-0.17	-0.04	-0.20	-0.07	0.04	0.45	2.23	1.59	50
49	0.13	0.32	0.52	-0.32	-0.23	-0.40	-0.48	-0.17	0.00	0.42	0.36	0.35	49
48	0.60	0.42	0.58	0.25	-0.04	-0.03	-0.14	-0.03	0.06	0.53	0.53	0.93	48
47	0.53	0.48	0.12	0.05	-0.06	-0.08	-0.06	-0.14	-0.08	0.29	0.37	0.83	47
46	0.46	0.63	0.75	0.35	-0.12	-0.08	-0.27	-0.25	0.00	0.18	0.66	1.10	46
45	0.45	0.35	0.36	0.03	-0.20	-0.23	-0.23	-0.39	-0.08	0.21	0.84	0.68	45
44	0.64	0.31	0.47	-0.06	-0.14	-0.24	-0.35	-0.16	-0.12	0.27	0.54	0.82	44
43	0.50	0.20	-0.04	-0.14	-0.28	-0.26	-0.66	-0.48	-0.26	0.04	0.53	0.52	43
42	0.23	0.04	-0.07	-0.33	-0.75	-0.58	-1.23	-0.66	-0.53	-0.28	0.31	0.46	42
41	0.56	-0.10	-0.07	-0.62	-0.76	-0.67	-1.16	-0.33	-0.41	-0.12	-0.05	0.32	41
40	0.67	-0.10	-0.11	-0.83	-1.06	-0.96	-1.34	-1.17	-0.90	-0.18	0.42	0.42	40
39	-0.14	-0.32	-0.55	-0.76	-1.47	-1.33	-1.48	-1.23	-0.81	-0.67	-0.05	-0.29	39
38	-0.05	-0.37	-0.53	-0.83	-0.85	-0.97	-0.64	-0.71	-0.48	-0.37	-0.37	-0.05	38
37	-0.07	-0.37	-0.44	-0.61	-0.77	-0.71	-0.49	-0.55	-0.50	-0.36	-0.15	-0.09	37
36	-0.34	-0.56	-0.79	-0.86	-1.17	-1.22	-0.88	-0.86	-0.80	-0.60	-0.42	-0.38	36
35	-0.28	-0.44	-0.71	-0.93	-0.97	-0.96	-0.78	-0.80	-0.62	-0.53	-0.32	-0.30	35
34	-0.09	-0.13	-0.27	-0.25	-0.27	-0.19	-0.19	-0.18	-0.20	-0.11	-0.11	-0.08	34
33	-0.18	-0.24	-0.33	-0.31	-0.29	-0.21	-0.22	-0.24	-0.26	-0.22	-0.22	-0.21	33
32	-0.14	-0.17	-0.25	-0.26	-0.25	-0.16	-0.18	-0.20	-0.21	-0.25	-0.18	-0.21	32
31	-0.31	-0.41	-0.52	-0.53	-0.54	-0.47	-0.44	-0.43	-0.45	-0.40	-0.36	-0.36	31
30	-0.45	-0.51	-0.66	-0.65	-0.71	-0.61	-0.49	-0.49	-0.54	-0.52	-0.43	-0.39	30
29	-0.52	-0.64	-0.98	-0.66	-1.20	-0.81	-0.69	-0.54	-0.73	-0.59	-0.45	-0.66	29
28	-0.45	-0.61	-0.73	-0.76	-0.78	-0.68	-0.52	-0.52	-0.56	-0.57	-0.51	-0.45	28
27	-0.40	-0.50	-0.63	-0.69	-0.81	-0.72	-0.52	-0.48	-0.50	-0.49	-0.39	-0.37	27
26	-0.44	-0.46	-0.65	-0.74	-0.75	-0.67	-0.43	-0.45	-0.42	-0.51	-0.45	-0.43	26
25	-0.35	-0.48	-0.61	-0.70	-0.72	-0.61	-0.40	-0.39	-0.40	-0.46	-0.38	-0.35	25
24	-0.26	-0.39	-0.54	-0.65	-0.69	-0.58	-0.32	-0.34	-0.26	-0.40	-0.37	-0.28	24
23	-0.33	-0.41	-0.57	-0.63	-0.66	-0.56	-0.31	-0.25	-0.22	-0.39	-0.34	-0.31	23
22	-0.31	-0.31	-0.42	-0.66	-0.63	-0.63	-0.21	-0.18	-0.24	-0.30	-0.29	-0.27	22
21	-0.32	-0.27	-0.41	-0.60	-0.53	-0.45	-0.14	-0.21	-0.04	-0.24	-0.19	-0.20	21
	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	

Figure 13.—Seasonal cycle of alongshore surface wind stress near the coast. Means of the alongshore components of wind stress were computed by month for the 1-degree squares immediately adjacent to the coast. Units are dyne cm^{-2}. The contour interval is 0.5 dyne cm^{-2}. Equatorward alongshore stress is shaded. Numbers along ordinate are degrees north latitude.



	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	
50	0.02	0.18	0.28	-0.05	0.11	0.15	0.03	0.04	0.00	-0.07	-2.10	0.05	50
49	0.22	0.20	0.16	0.08	0.11	0.14	0.07	0.03	-0.01	0.09	0.29	0.47	49
48	0.41	0.13	0.23	0.31	0.17	0.15	0.22	0.11	0.10	0.08	0.08	0.31	48
47	-0.17	-0.18	0.14	0.27	0.16	0.10	0.11	0.08	0.07	-0.08	-0.20	-0.22	47
46	-0.00	0.07	0.10	0.34	0.39	0.22	0.27	0.16	0.05	-0.08	-0.19	0.03	46
45	0.04	0.23	0.33	0.24	0.14	0.16	0.10	0.07	0.10	0.05	0.01	0.01	45
44	-0.01	0.06	0.35	0.08	0.15	0.10	0.06	0.05	0.08	0.03	-0.02	0.22	44
43	0.10	0.03	0.33	0.06	0.15	0.08	0.13	0.16	0.03	0.00	0.05	0.07	43
42	0.21	0.08	0.11	0.03	0.00	0.01	0.00	0.00	-0.19	-0.05	-0.02	-0.06	42
41	0.00	0.10	0.20	0.27	0.48	0.44	0.68	0.20	0.19	0.12	0.07	-0.01	41
40	0.08	-0.08	-0.21	-0.32	-0.51	-0.28	-0.51	-0.45	-0.31	-0.06	0.07	0.11	40
39	0.10	0.06	0.16	0.19	0.34	0.28	0.24	0.22	0.13	0.10	0.01	0.11	39
38	0.00	0.12	0.25	0.38	0.33	0.33	0.23	0.27	0.15	0.08	0.09	-0.05	38
37	0.05	0.03	0.12	0.14	0.14	0.16	0.16	0.11	0.09	0.04	0.05	0.00	37
36	-0.02	-0.02	-0.03	-0.05	-0.03	-0.08	0.00	-0.05	-0.09	-0.06	-0.07	-0.04	36
35	0.07	0.12	0.19	0.30	0.33	0.31	0.24	0.20	0.17	0.15	0.07	0.05	35
34	-0.07	-0.02	0.06	0.08	0.10	0.07	0.05	0.05	0.05	0.02	-0.03	-0.05	34
33	0.08	0.16	0.22	0.27	0.24	0.20	0.19	0.19	0.17	0.12	0.10	0.04	33
32	0.06	0.08	0.15	0.19	0.20	0.16	0.15	0.15	0.11	0.14	0.05	0.06	32
31	0.05	0.09	0.17	0.18	0.21	0.18	0.15	0.15	0.12	0.10	0.06	0.01	31
30	0.05	0.11	0.16	0.19	0.26	0.17	0.13	0.11	0.11	0.09	0.07	0.05	30
29	-0.12	0.05	0.08	-0.01	0.09	0.02	0.03	0.00	0.04	-0.02	-0.16	0.00	29
28	-0.07	-0.10	-0.03	0.02	0.02	0.02	0.02	0.01	-0.02	-0.02	-0.07	-0.11	28
27	-0.19	-0.19	-0.11	-0.06	-0.09	-0.05	0.00	-0.04	-0.07	-0.09	-0.17	-0.14	27
26	-0.10	-0.07	0.00	0.06	0.08	0.08	0.05	0.09	0.06	0.00	-0.07	-0.10	26
25	-0.10	-0.07	-0.02	0.03	0.05	0.06	0.08	0.06	0.02	0.00	-0.06	-0.08	25
24	-0.13	-0.09	-0.03	0.02	0.07	0.10	0.07	0.10	0.09	0.00	-0.10	-0.10	24
23	-0.19	-0.12	-0.02	0.00	0.06	0.09	0.05	0.01	0.03	-0.03	-0.10	-0.19	23
22	-0.18	-0.11	-0.09	-0.09	-0.03	0.07	-0.01	0.01	-0.02	-0.01	-0.15	-0.24	22
21	-0.21	-0.19	-0.12	-0.16	-0.08	-0.06	-0.13	-0.03	-0.05	-0.24	-0.20	-0.21	21
	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC	

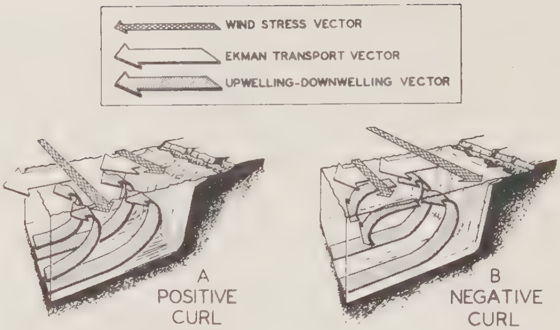


Figure 15.—A conceptual diagram of the relationship of wind stress curl to the divergence and convergence of surface Ekman transport offshore of the primary coastal upwelling zone.

Direct measurements of wind stress curl are not available; however, the curl of the monthly mean surface wind stress fields has been computed. The vertical component of the curl of the wind stress in spherical coordinates is defined by:

$$\vec{k}\cdot(\nabla\times\vec{\tau}) = \frac{1}{R\cos\varphi}\left[\frac{\partial\bar{\tau}_y}{\partial\lambda} - \frac{\partial}{\partial\varphi}(\bar{\tau}_x\cos\varphi)\right] \tag{7}$$

where R is the radius of the earth, φ and λ denote geographic latitude and longitude, respectively, and $\bar{\tau}_x$ and $\bar{\tau}_y$ denote the eastward and northward components of the mean surface wind stress. A finite difference equation approximating the curl at the grid point (i, j) in Figure 16 is given by:

$$\vec{k}\cdot(\nabla\times\bar{\tau})_{i,j} = \frac{1}{R\cos\varphi_j}\left[\frac{\bar{\tau}_{y\,i+1,j}-\bar{\tau}_{y\,i-1,j}}{2\Delta\lambda} - \left(\frac{(\bar{\tau}_x\cos\varphi)_{i,j+1}-(\bar{\tau}_x\cos\varphi)_{i,j-1}}{2\Delta\varphi}\right)\right] \tag{8}$$

where $\Delta\varphi = \Delta\lambda = 1°$. The method is similar to calculations described by Hantel (1970). Centered differences were utilized throughout the interior of the data grid. Forward and backward differences were required along the boundaries. As a result, certain artificial features may have been introduced at these boundaries.

Monthly Curl Distributions

Monthly fields of surface wind stress curl are displayed in Appendix III (Charts 37 to 48). These distributions correspond to the monthly mean wind stress distributions shown in Appendix I. Values are plotted in units of dyne cm^{-2} per 100 km. A value of 1 dyne cm^{-2}

Figure 14.—Seasonal cycle of onshore surface wind stress near the coast. Means of the onshore components of wind stress were computed by month for the 1-degree squares immediately adjacent to the coast. Units are dyne cm^{-2}. The contour interval is 0.5 dyne cm^{-2}. Offshore stress is shaded. Numbers along ordinate are degrees north latitude.

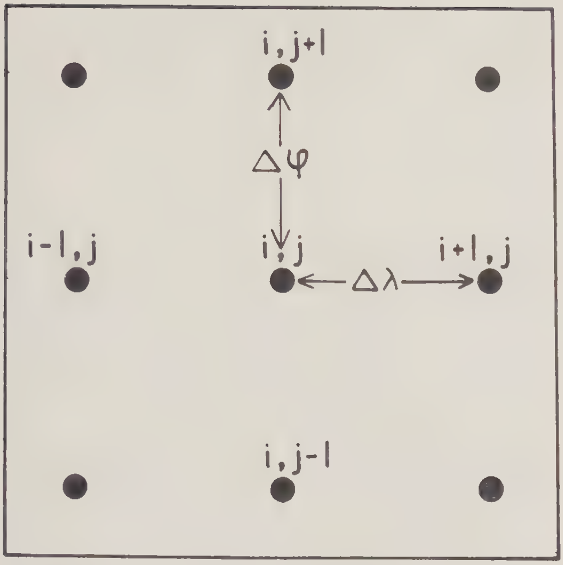


Figure 16.—Discretization grid used in calculating the wind stress curl.

per 100 km is equivalent to 1×10^{-7} dyne cm^{-3}. Negative values of wind stress curl are shaded.

Small scale features evident in these distributions should be viewed with caution. Detail within a single 1-degree square area which is not supported by similar values in surrounding squares probably reflects "noise" in the monthly means of surface wind stress. Objective smoothing procedures applied to the monthly mean wind stress fields would result in more homogeneous distributions of wind stress curl. A particular method has been described by Evenson and Veronis (1975).

Characteristic absolute magnitudes of the spatially averaged wind stress curl are 1×10^{-8} dyne cm^{-3}. This value is approximately a factor of two less than the summertime mean reported by Halpern (1976) for an upwelling region near the Oregon coast. Considering the time and space averages used in the present study, this difference appears to be reasonable. However, the values are consistent with wind stress curl calculations reported by Saunders (1976). The probable errors associated with these estimates of wind stress curl may be calculated from a knowledge of the spatial distributions of standard errors of the (wind stress) component means (see Appendix II). On average, the expected error is 1×10^{-8} dyne cm^{-3}, with maximum and minimum errors of 4×10^{-8} dyne cm^{-3} and 1×10^{-10} dyne cm^{-3}, respectively. Of course, these values apply to particular individual 1-degree squares. Large values generally correspond to "holes" in the distributions, which are easily seen in the monthly charts. For larger space scales, errors associated with the gradients of the mean wind stress components would tend to cancel. Thus, greater confidence may be expected for the patterns of wind stress curl which are consistent over several degrees of latitude and longitude.

The large-scale features of positive and negative curl along the coast are significant. Important details to note are the sign of the wind stress curl at the coast, and the position of the line of zero wind stress curl. A general feature common to all months is the occurrence, on average, of positive wind stress curl near the coast, and negative curl at some distance offshore. This feature is well developed from May to September. Greater spatial variability is evident in winter distributions.

Existence of an offshore wind stress maximum results in a line of zero wind stress curl approximately parallel to the coast. Positive curl occurs inshore of the maximum wind stress. Negative curl in the offshore region is associated with the anticyclonic atmospheric circulation over the interior ocean. The positive curl near the coast is related to topography and to local features in the surface wind stress distributions.

The distributions from December to March are characterized by positive wind stress curl near the coast from San Francisco to northern Baja California, and south of Punta Eugenia. Large areas of associated Ekman divergence extend several hundred kilometers off the coast. The patterns of wind stress curl are less well behaved near the coasts of Oregon and Washington. However, negative wind stress curl near this coastal region appears to be typical of the distributions during the winter.

During spring and summer upwelling seasons, the dominant patterns of surface wind stress curl are easily recognized. The line of zero wind stress curl parallels the coast approximately 200 to 300 km offshore, along the entire boundary from northern Baja California to Vancouver Island, and from June through September. Yoshida and Mao (1957) placed this line at approximately 500 km from the coast. Considering the coarse resolution (5-degree squares of latitude and longitude) of their data, this disparity is not surprising.

The months of April-May and October-November appear as transitional periods. During transition from spring to summer, the negative curl along the coasts of Oregon and Washington shifts to positive curl. The offshore distribution takes on a more uniform character. Scattered regions of positive and negative curl are replaced by a large area of negative curl. The late fall transition is marked by a total breakdown in the curl distributions within the northern sector of the grid.

Several local (positive) curl maxima are associated with major topographic changes in the coastline configuration. Large values of positive wind stress curl are found near Cape Blanco, Cape Mendocino, San Francisco, and Point Conception. These features may be real, or they may be artifices of the finite difference calculations or the data distributions. However, one does note that near Point Conception, the values of positive wind stress curl are consistent with a decrease in the magnitude of the surface wind stress in the lee of the point. Where areas of positive wind stress curl extend offshore of capes, there would tend to be a continued, although much reduced, level of upwelling outside of the primary coastal upwelling regime.

A region of negative wind stress curl (Ekman convergence) reaches the coast of Baja California between Punta Eugenia and Punta Baja to the north. This feature appears consistently throughout the year. A partial breakdown in this system occurs in August, October, and November. However, considering the probable uncertainties in these derived data, one might reasonably conclude that the coastal region near Punta Eugenia can be characterized in the mean by convergence in the surface wind drift. The distributions of wind stress curl in this area imply favorable conditions for formation of fronts and convergent patches of recently upwelled water.

Coastal Time Series

The mean annual cycle of wind stress curl near the coast is shown in Figure 17. Positive wind stress curl occurs along most of the coast throughout the year. Exceptions to this generalization are found in the region south of lat. 30°N and between lat. 40°N and 47°N. The temporal persistence of the negative wind stress curl near Punta Eugenia (lat. 29°N) is clearly seen in this time series. A similar feature occurs near the tip of Baja California. Seasonal variation between positive and negative curl is apparent from Cape Mendocino to the Columbia River.

Yoshida and Mao (1957) presented evidence indicating that open-ocean upwelling is related to wind stress curl. This process is distinct from coastal upwelling which is primarily a boundary phenomenon. However, the two mechanisms are not totally independent. In regions where positive wind stress curl occurs, such as between lat. 30°N and 40°N throughout the year, and near the coasts of Oregon and Washington during the summer, ascending motion related to the wind-induced divergence offshore enhances the upwelling associated with the more dominant coastal divergence.

DISCUSSION

Monthly distributions of surface wind stress show an offshore maximum which progressively develops over a large extent of the California Current and shifts northward and intensifies from winter to summer. This process is a primary forcing function for coastal upwelling. Off Baja California, wind-induced surface divergence occurs on average throughout the year. Downwelling occurs near the coast of Vancouver Island, except during the restricted period between May and August when a small equatorward component of surface wind stress is observed.

The major seasonal variations in the magnitude and direction of the surface wind stress can be described

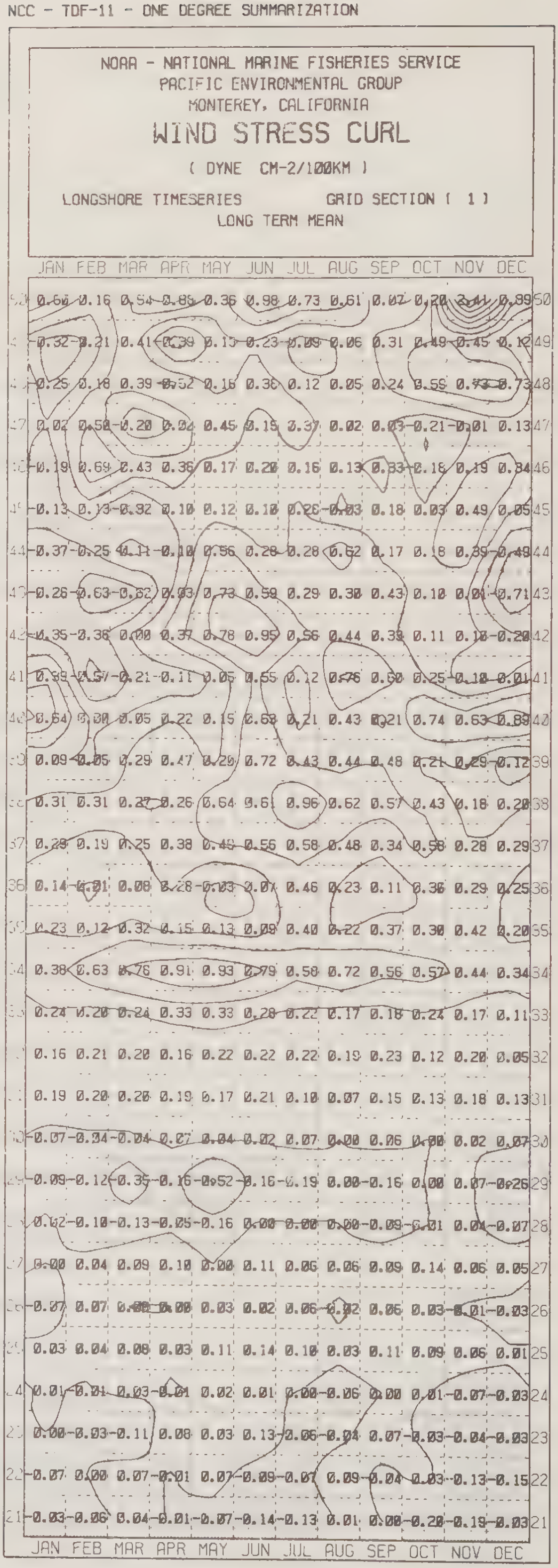


Figure 17.—Seasonal cycle of wind stress curl near the coast. The wind stress curl is shown by month for the 1-degree squares immediately adjacent to the coast. The calculations were based on the monthly mean surface wind stress distributions. Units are dyne cm^{-2} per 100 km. The contour interval is 0.25 dyne cm^{-2} per 100 km. Negative values are shaded. Numbers along ordinate are degrees north latitude.

simply in terms of the general atmospheric circulation over the northeast Pacific Ocean. Monthly mean surface pressure charts typically show two well-developed pressure cells. A high pressure system over the ocean shifts northward and increases in strength from winter to summer. The center of the cell moves in a northwestward direction. This shift in the large-scale anticyclonic circulation results in the observed winter to summer reversal in the alongshore component of wind off the coasts of Oregon and Washington. A low pressure system is situated over the southwestern United States. This semipermanent thermal low is fully developed over the Central Valley in California during the summer. Cyclonic circulation associated with the low leads to equatorward surface wind stress parallel to the coast. The amplitude of the annual cycle is large. During winter, both of these pressure cells weaken. The high pressure system moves southward and the coasts of Oregon and Washington come under the influence of the intense low pressure system in the Gulf of Alaska.

The primary mechanism controlling the location and strength of the wind stress maximum and the associated coastal upwelling is described by seasonal variations in the gradient between the two pressure cells. During the winter, this gradient is weak. Strong heating over the continent during summer deepens the low and increases the amplitude of the onshore-offshore pressure gradient. As a result of the northward shift and strengthening of the high, and deepening of the low, the region of maximum wind stress moves from the area south of Point Conception to the vicinity of Cape Mendocino. These variations are, of course, a function of differential ocean-continent heating related to the annual cycle of solar radiation.

Physical Implications

Climate of the adjacent coastal regions is influenced by upwelling. During summer, the dome of high pressure which develops over the North Pacific Ocean favors large-scale subsidence and a strong temperature inversion over the west coast of the United States. This suppresses deep cloud formation and greatly inhibits precipitation. Unpublished distributions of cloud cover,[6] summarized from ship observations, show a large onshore-offshore gradient in the total cloud amount. Minima occur at the coast. The effect of the large-scale subsidence is noted in the true desert climate of Baja California, and in the almost complete lack of rainfall along the coasts of California, Oregon, and Washington during the summer. Coastal upwelling primarily influences the local climate of the nearshore zone within 10 to 20 km of the coast and contributes to the formation of low stratus clouds and fog typical of much of the coast along California and Oregon.

A secondary mechanism may account for local intensification of surface wind stress and persistence of coastal upwelling over periods ranging from several weeks to a few months (Bakun 1974). In a simplified positive feedback model, wind stress parallel to the coast brings cold water to the surface and cools the adjacent air. The resulting temperature contrast between the continent and the ocean increases the local pressure gradient. Alongshore surface winds are increased and upwelling is enhanced (Ramage 1971). This mechanism may be slightly modified by the effect of atmospheric stability. In the summertime coastal upwelling zone, the air-sea temperature difference is usually positive. This stable stratification decreases the magnitude of the surface wind stress. The resulting negative feedback may partially offset the increase in surface winds associated with the described changes in the local pressure gradient.

The existence of maximum wind stress some 200 to 300 km from the coast is an interesting feature. Of course, a maximum in the onshore-offshore pressure gradient offshore may explain this phenomenon. Positive feedback associated with wind-induced upwelling extending hundreds of kilometers off the coast may act to intensify the alongshore winds. However, this feature also suggests a coastal boundary layer which acts to frictionally retard the winds near the coast, leading to a positive wind stress curl in the nearshore region.

A characteristic feature of the wind stress curl distributions is the occurrence of a line of zero curl at some distance from the coast. Observations show positive curl inshore of this line and negative curl in the offshore region. A theoretical analysis suggests that a poleward undercurrent along an eastern boundary is favored by positive wind stress curl along the coast and a poleward decrease in surface heating (Pedlosky 1974a). The monthly distributions of wind stress curl presented in this study are generally consistent with an equatorward Sverdrup flow offshore and a poleward Sverdrup flow near the coast, except in the region from Punta Eugenia to Punta Baja, where the wind stress curl is negative. The general pattern of positive wind stress curl along the coast and observations of the California Countercurrent (Wooster and Jones 1970; Wickham 1975) are consistent with Pedlosky's theory.

The Sverdrup transport balance expressed in Equation (6) may provide a simple and reasonable explanation for the existence of the current-countercurrent system observed along the west coast of the United States. Transport calculations, based on the July wind stress curl data for the line of 1-degree squares extending offshore of Cape Blanco (lat. 43°N), show a net southward transport of 3.5×10^{12} g s^{-1}. Within 300 km of the coast, an integrated northward transport of 2.2×10^{12} g s^{-1} is required. Negative wind stress curl between long. 127°W and 133°W is associated with a southward vertically integrated mass transport of 5.7×10^{12} g s^{-1}. These values underestimate, by a factor of two, the total volume transport of 10 sv (1 sverdrup = 10^6 m^3 s^{-1}) for the California Current suggested by Sverdrup et al. (1942:724).

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[6] Distributions of monthly mean cloud cover over the California Current are on file at Pacific Environmental Group, National Marine Fisheries Service, NOAA, Monterey, CA 93940.

A relationship between wind stress curl and the California Current system has been suggested. The data indicate that the poleward undercurrent observed along the west coast of North America may be driven locally by positive wind stress curl. However, a possibility does exist that the boundary current is not entirely the result of local forcing. Coastal areas may respond to wavelike disturbances propagating from other regions of the ocean (Wyrtki 1975), or to other nonlocal processes (Pedlosky 1974b).

Biological Implications

Relationships among patterns of coastal and equatorial upwelling and distributions of primary production have been discussed by Cushing (1969). Favorable conditions for phytoplankton growth are maintained within surface photic layers by upwelling of nutrient-rich subsurface water. Offshore divergence related to the curl of the wind stress effectively extends the width of the biological upwelling zone. Fronts may form in areas of negative wind stress curl just offshore of the primary coastal convergence, such as near Punta Eugenia. These fronts would tend to concentrate both the available food and the grazers within the same areas. This process may be important to survival of fish stocks which spawn in this coastal region.

Seasonal changes in surface circulation may also provide mechanisms for survival and possible separation of stocks along the coast. The current-countercurrent system characteristic of southern California suggests a mechanism whereby pelagic fish could migrate seasonally from primary feeding grounds within the coastal upwelling regime off northern California to spawning grounds off Baja California.

A general requirement for vertically integrated northward Sverdrup transport along the coast apparently breaks down near Punta Eugenia where negative wind stress curl is observed (Fig. 18A). In this region, there must be southward vertically integrated Sverdrup transport.

With this consideration in mind, it is interesting to note the winter distribution of surface currents depicted in Figure 18B. The large-scale pattern suggests two separate cyclonic gyres associated with positive wind stress curl in the Southern California Bight, and south of Punta Eugenia. In the region of negative wind stress curl, the indicated surface flow is toward the south.

The importance of coastal upwelling, offshore divergence, and patterns of surface circulation to the early survival of larvae in the California Current region has been recognized (Anonymous 1952). The correspondences of features in the patterns of wind stress curl, surface currents, and winter distributions of the northern anchovy, *Engraulis mordax*, (Vrooman and Smith, 1971), shown in Figure 18C, are highly suggestive of larval transport mechanisms which could lead to formation of subpopulations of pelagic fishes in the California Current. These mechanisms have been described by

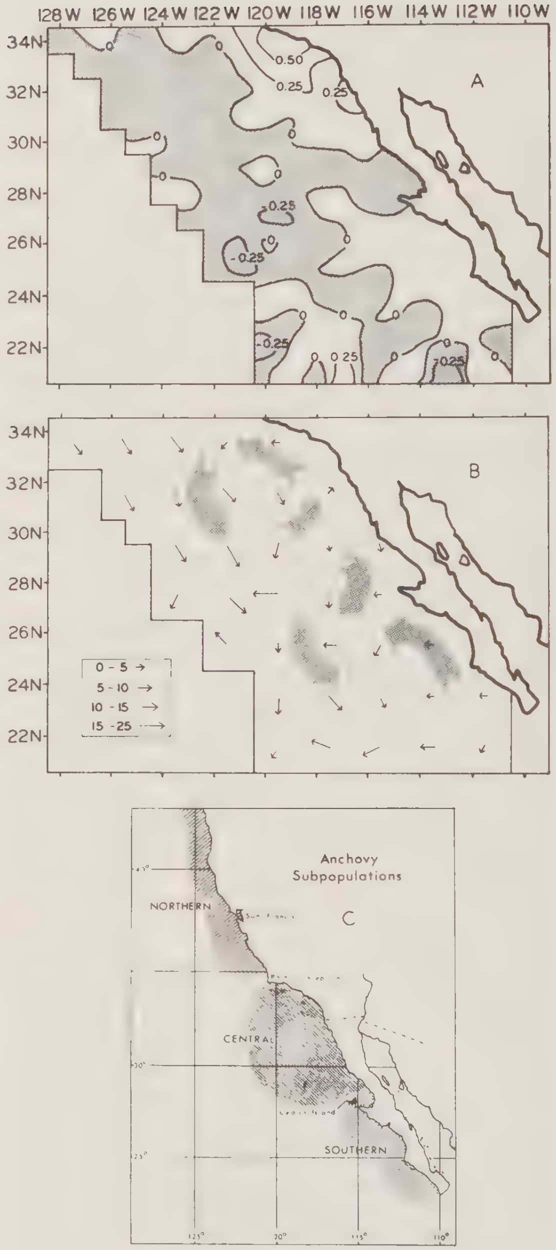

Figure 18.—Distributions of: A. wind stress curl, B. surface currents, and C. anchovy subpopulations. Wind stress curl is shown for September. Units are dyne cm $^{-2}$ per 100 km. The contour interval is 0.25 dyne cm $^{-2}$ per 100 km. Negative values are shaded. The winter distribution of surface currents is depicted in terms of 2-degree summarizations of ship drift data. Vector symbols are scaled according to the key on the chart. Units are cm s $^{-1}$. Large arrows suggest the split cyclonic circulation which develops off southern California and Baja California. The winter distributions of the three subpopulations of northern anchovy are shown in the bottom figure. Figure C is after Vrooman and Smith (1971).

Parrish (1976). Distributions of Pacific mackerel, *Scomber japonicus*, are similar to those for central and southern subpopulations of northern anchovy shown in Figure 18C.

CONCLUSIONS

The present study has demonstrated the utility of historical marine observations in describing details of surface properties over an area of the North Pacific Ocean. Resolution by 1-degree square and long-term month is feasible when the amplitude of the seasonal cycle is large. This method of summarization may fail in regions of sparse data, or in the tropics where long-term fluctuations frequently obscure the seasonal cycle.

Summarization of these data by 1-degree square, month, and year often fails to produce consistent time series. The resulting fields may not be statistically significant if the mean values are based on too few observations. Objective analysis provides a method to obtain consistency in time and space. However, with these methods, continuity in time is gained at the expense of spatial resolution. An empirical approach might be used to calibrate the large-scale analyzed fields in terms of the features evident in higher resolution distributions, such as those presented in this report. The resulting time series could be related to fluctuations of marine biological communities which must respond to wide variations in environmental conditions on time scales ranging from a few days to several years.

ACKNOWLEDGMENTS

The author is indebted to Andrew Bakun for his original suggestions, constructive criticism, and continued encouragement throughout the course of this work. Gunter R. Seckel and David M. Husby provided invaluable advice, many stimulating discussions, and reviewed the completed manuscript. Grateful appreciation is extended to James H. Johnson for providing the opportunity to complete this research. All are colleagues at the Pacific Environmental Group, National Marine Fisheries Service, NOAA. Historical surface marine data and electronic computing and plotting facilities were provided by the U.S. Navy, Fleet Numerical Weather Central.

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APPENDIX I

Monthly Surface Wind Stress Distributions

The long term composite monthly mean surface wind stress distributions are displayed in Charts 1 to 12 as resultant vectors, in Charts 13 to 24 as the eastward components, and in Charts 25 to 36 as the northward components. The values are plotted in units of dyne cm^{-2}. The month is indicated in the figure legend in the upper right corner of the charts. The two years displayed below the month, for example 1858-1972, correspond to the year of the earliest report and the year of the most recent report, respectively. The coastline configuration is superimposed on the grid as a visual aid and does not represent a conformal mapping.

In Charts 1 to 12, the vectors are plotted according to the scale shown below the figure legend. The mean vector magnitudes are contoured at intervals of 0.5 dyne cm^{-2}. Magnitudes greater than 1.0 dyne cm^{-2} are shaded.

Charts 13 to 24 display contoured values of the eastward component of the resultant surface wind stress. The contour interval is 0.5 dyne cm^{-2}. Positive values correspond to eastward components. Negative values are shaded.

The northward component of the resultant stress is plotted in Charts 25 to 36. The contour interval is 0.5 dyne cm^{-2}. Positive values correspond to northward components. Negative values are shaded.

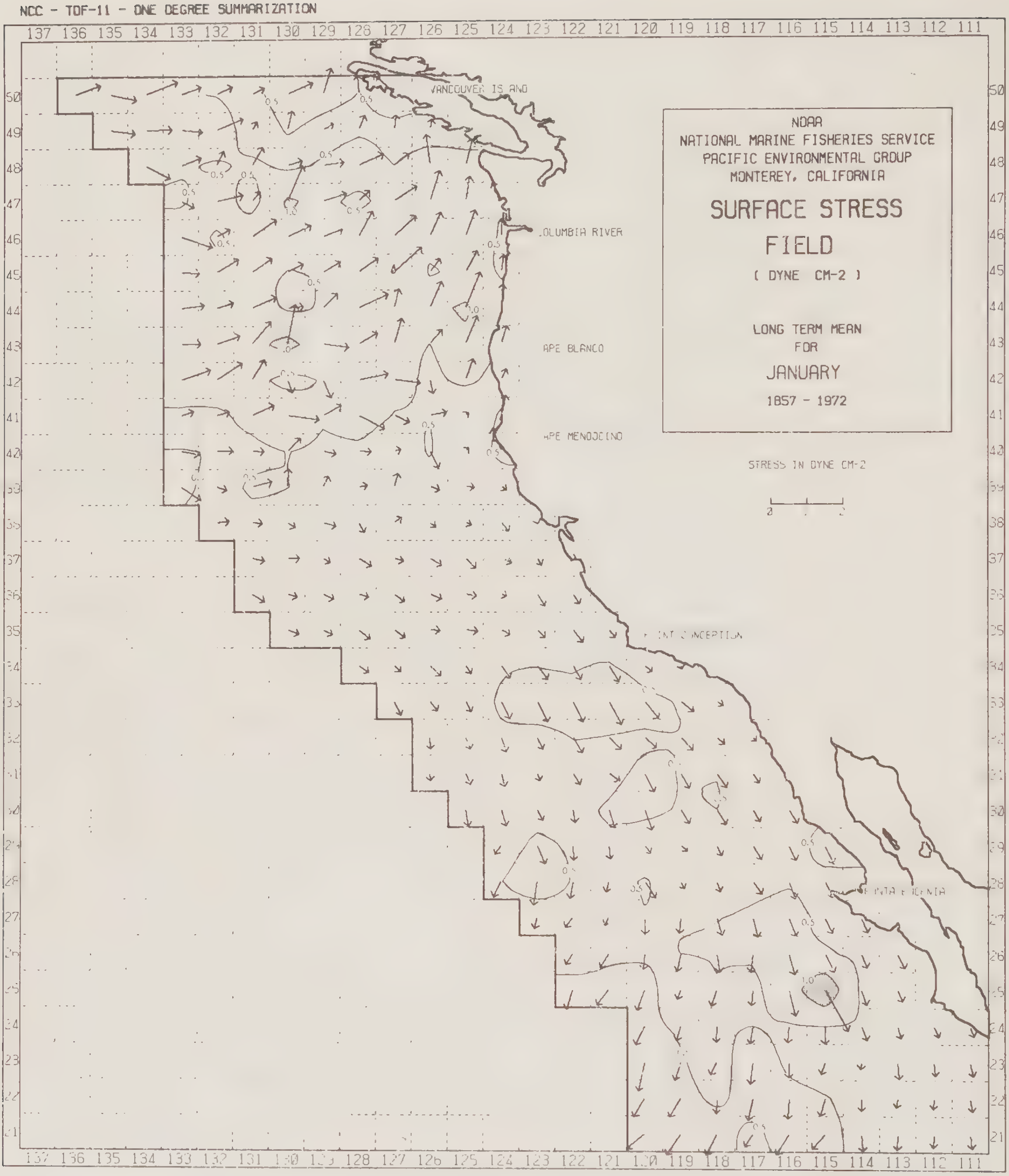
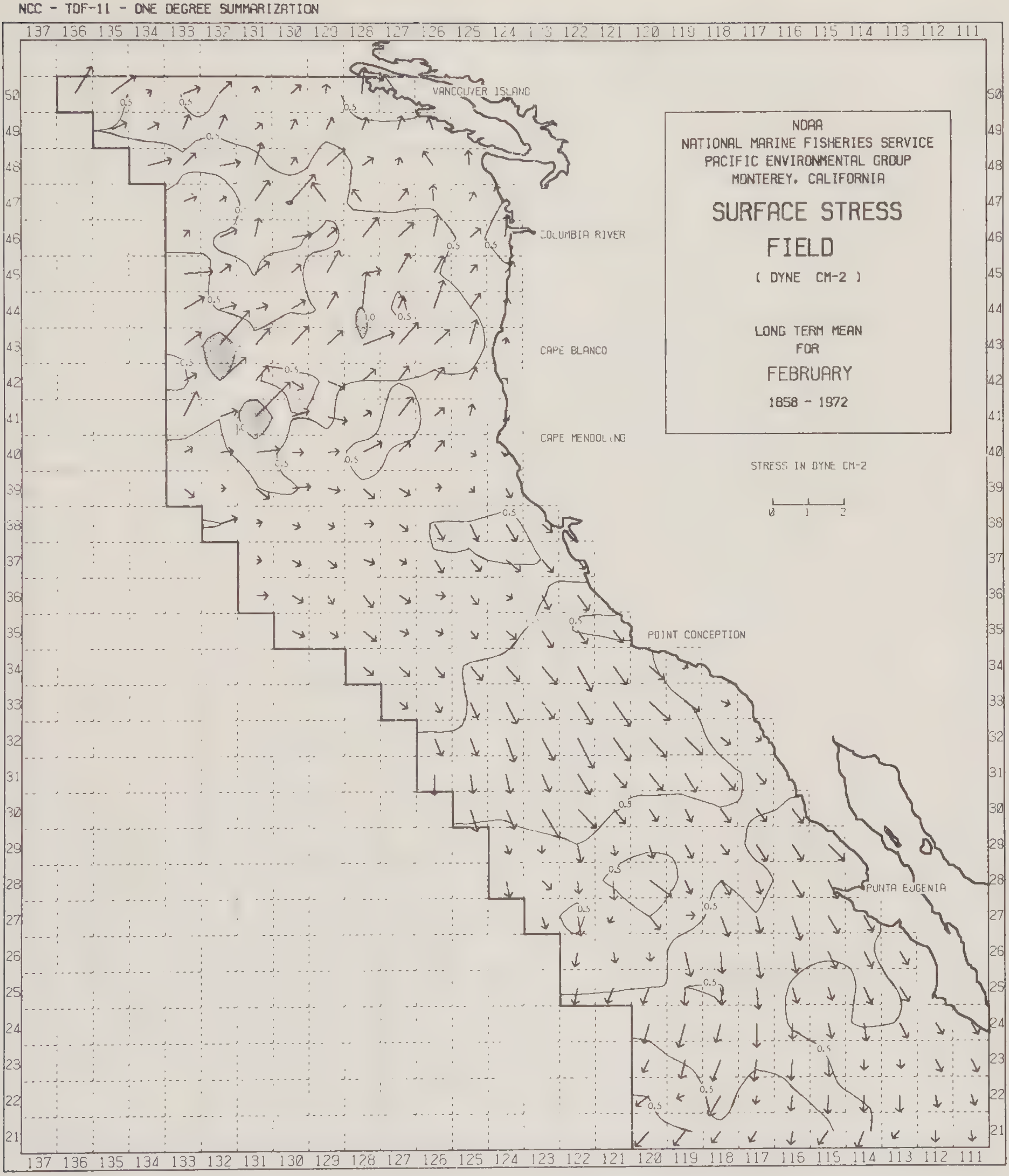

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
SURFACE STRESS FIELD
(DYNE CM-2)
LONG TERM MEAN FOR JANUARY
1857 - 1972
STRESS IN DYNE CM-2
0
2
VANCOUVER IS AND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
0.5
1.0
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21

Chart 1.—Resultant surface wind stress vectors for January.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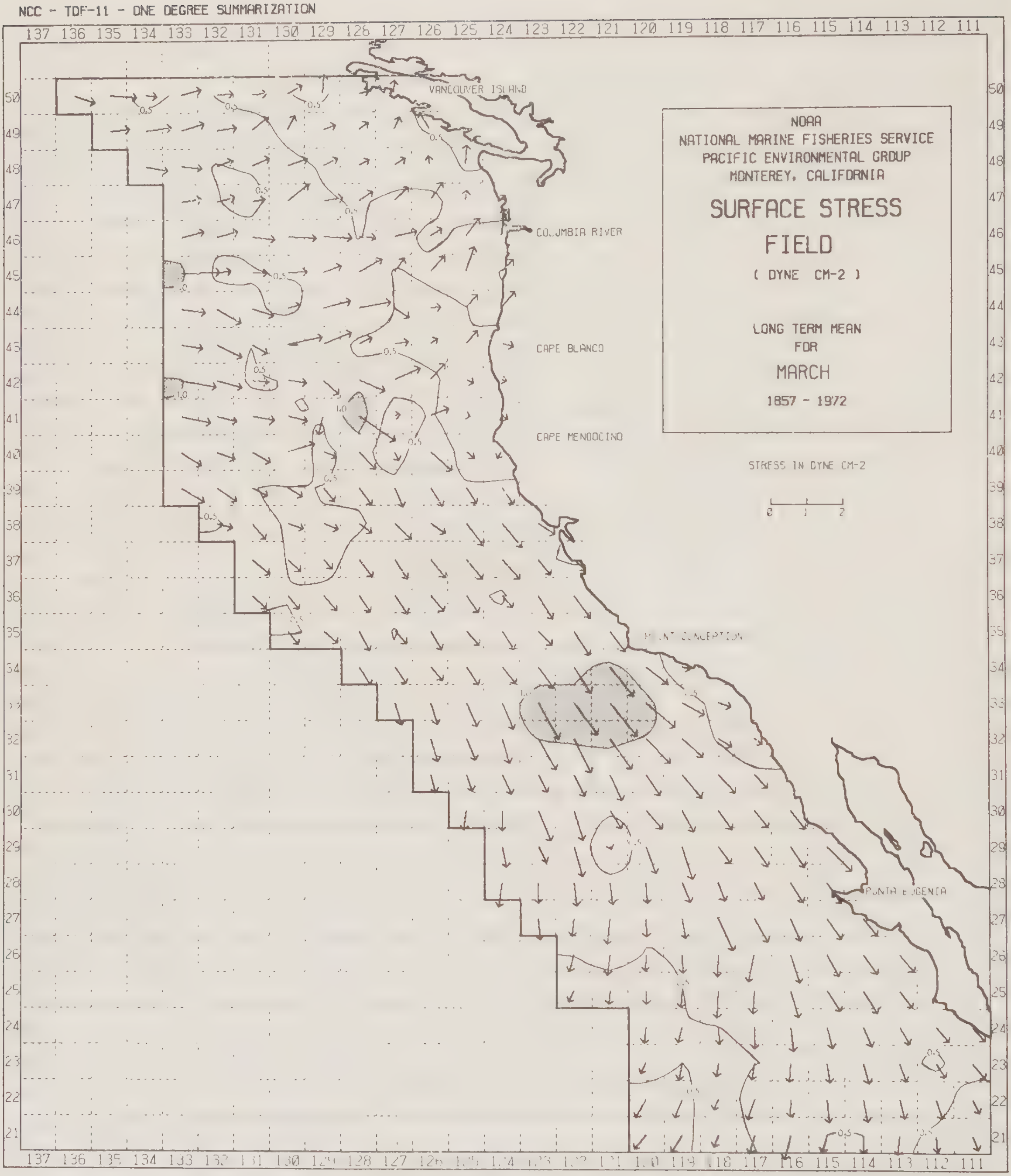
MONTEREY, CALIFORNIA
SURFACE STRESS
FIELD
(DYNE CM-2)
LONG TERM MEAN
FOR
FEBRUARY
1858 - 1972
STRESS IN DYNE CM-2
0 1 2
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
0.5
1.0
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21

Chart 2.—Resultant surface wind stress vectors for February.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137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
SURFACE STRESS
FIELD
(DYNE CM-2)
LONG TERM MEAN
FOR
MARCH
1857 - 1972
STRESS IN DYNE CM-2
0 1 2
0.5
1.0

Chart 3.—Resultant surface wind stress vectors for March.

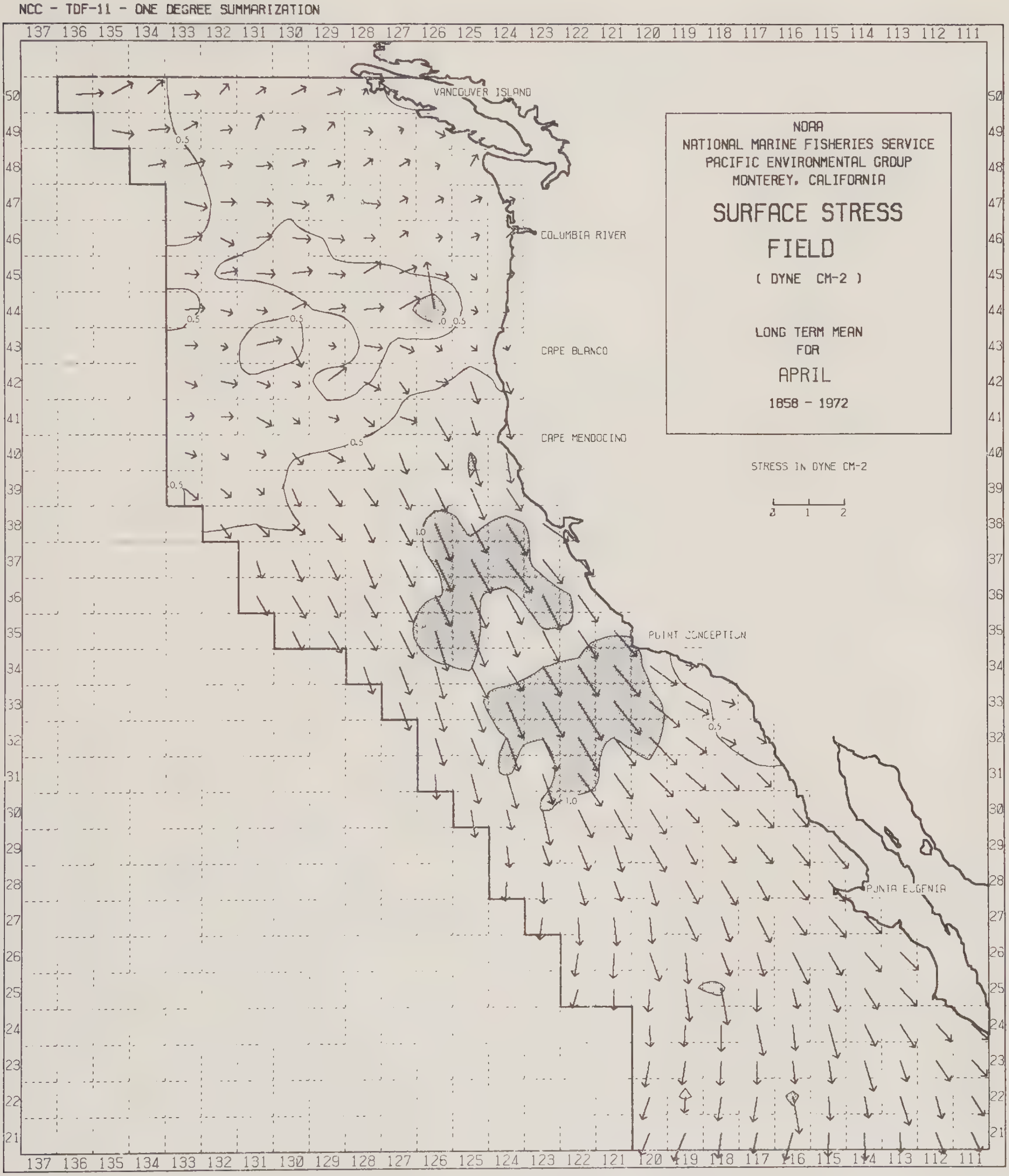
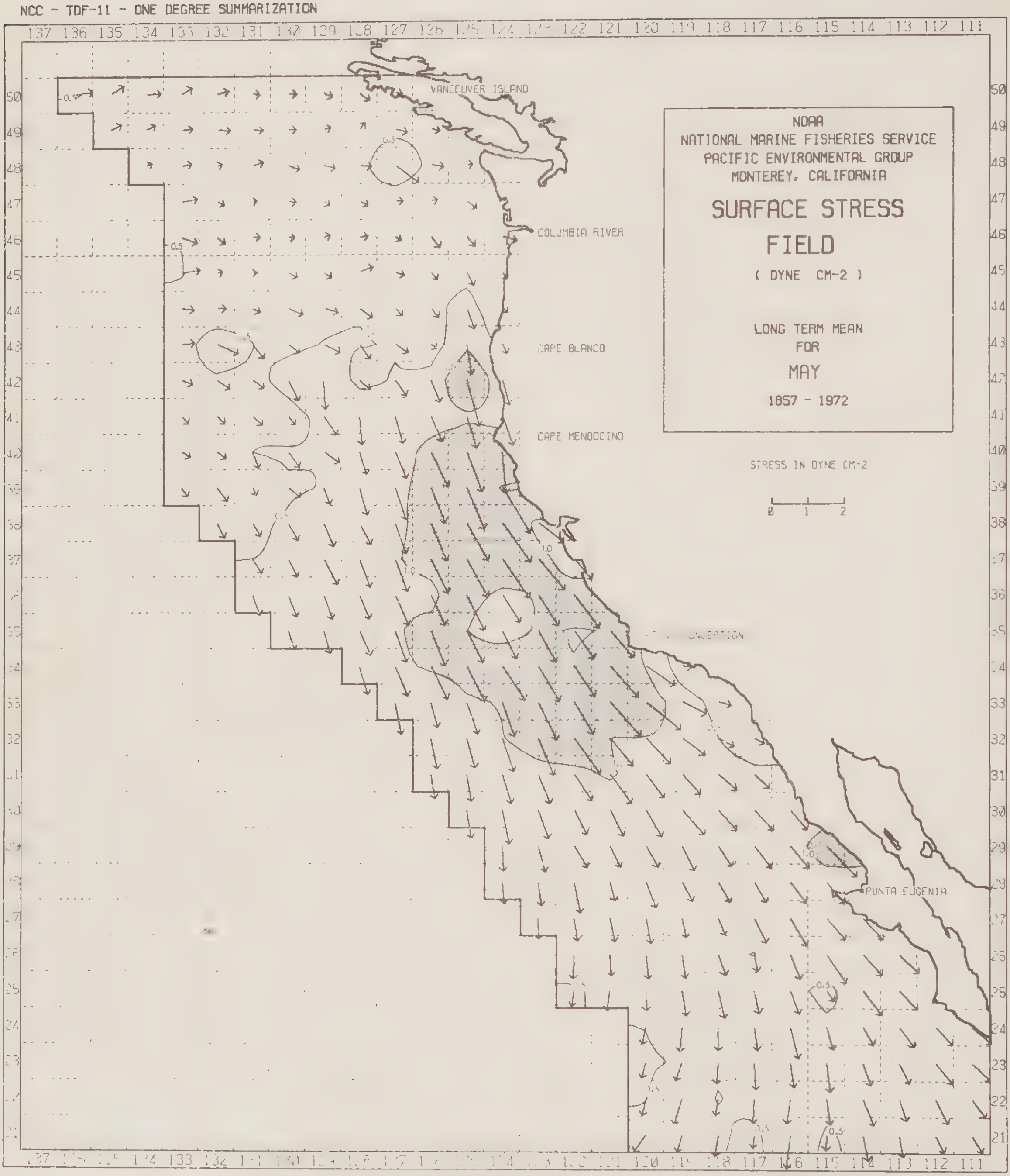

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
0.5
1.0
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
SURFACE STRESS FIELD
(DYNE CM-2)
LONG TERM MEAN FOR
APRIL
1858 - 1972
STRESS IN DYNE CM-2
0 1 2

Chart 4.—Resultant surface wind stress vectors for April.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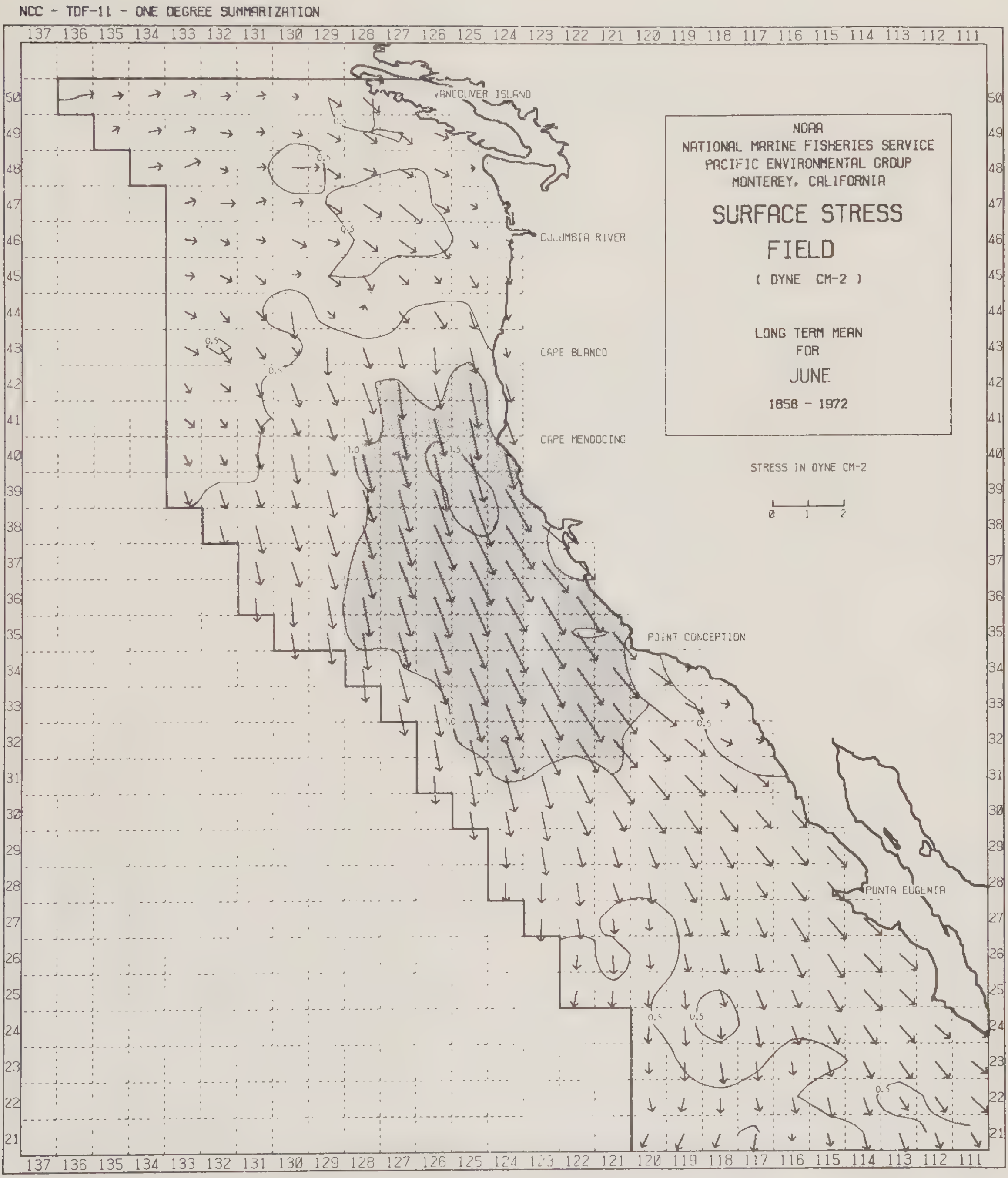
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
SURFACE STRESS
FIELD
(DYNE CM-2)
LONG TERM MEAN
FOR
MAY
1857 - 1972
STRESS IN DYNE CM-2
0
1
2
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
CONCEPTION
PUNTA EUGENIA
0.5
1.0
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21

Chart 5.—Resultant surface wind stress vectors for May.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NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
SURFACE STRESS
FIELD
(DYNE CM-2)
LONG TERM MEAN
FOR
JUNE
1858 - 1972
STRESS IN DYNE CM-2
0 1 2
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
0.5
1.0
1.5
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21

Chart 6.—Resultant surface wind stress vectors for June.

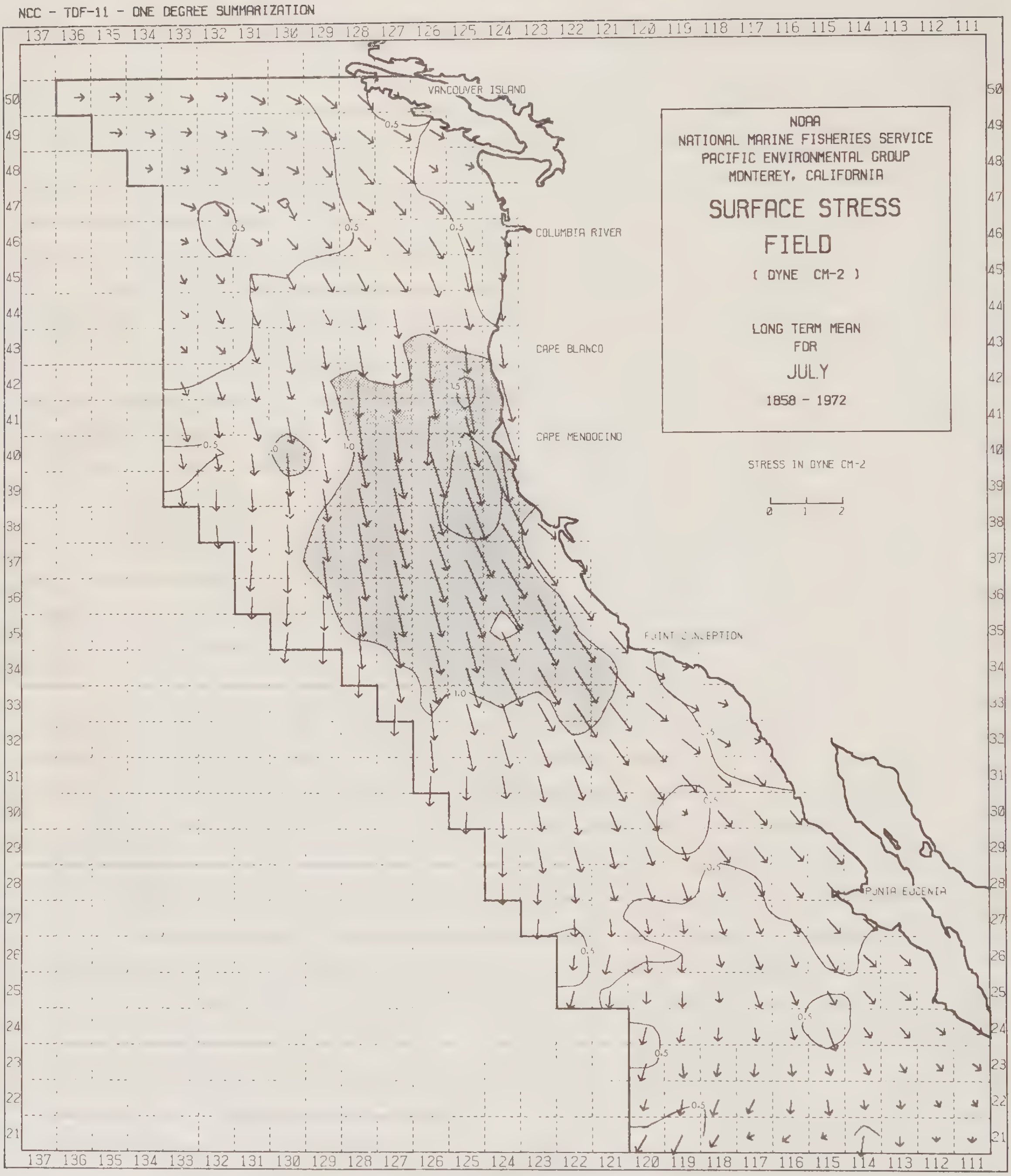

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
SURFACE STRESS
FIELD
(DYNE CM-2)
LONG TERM MEAN
FOR
JULY
1858 - 1972
STRESS IN DYNE CM-2
0 1 2
0.5
1.0
1.5

Chart 7.—Resultant surface wind stress vectors for July.

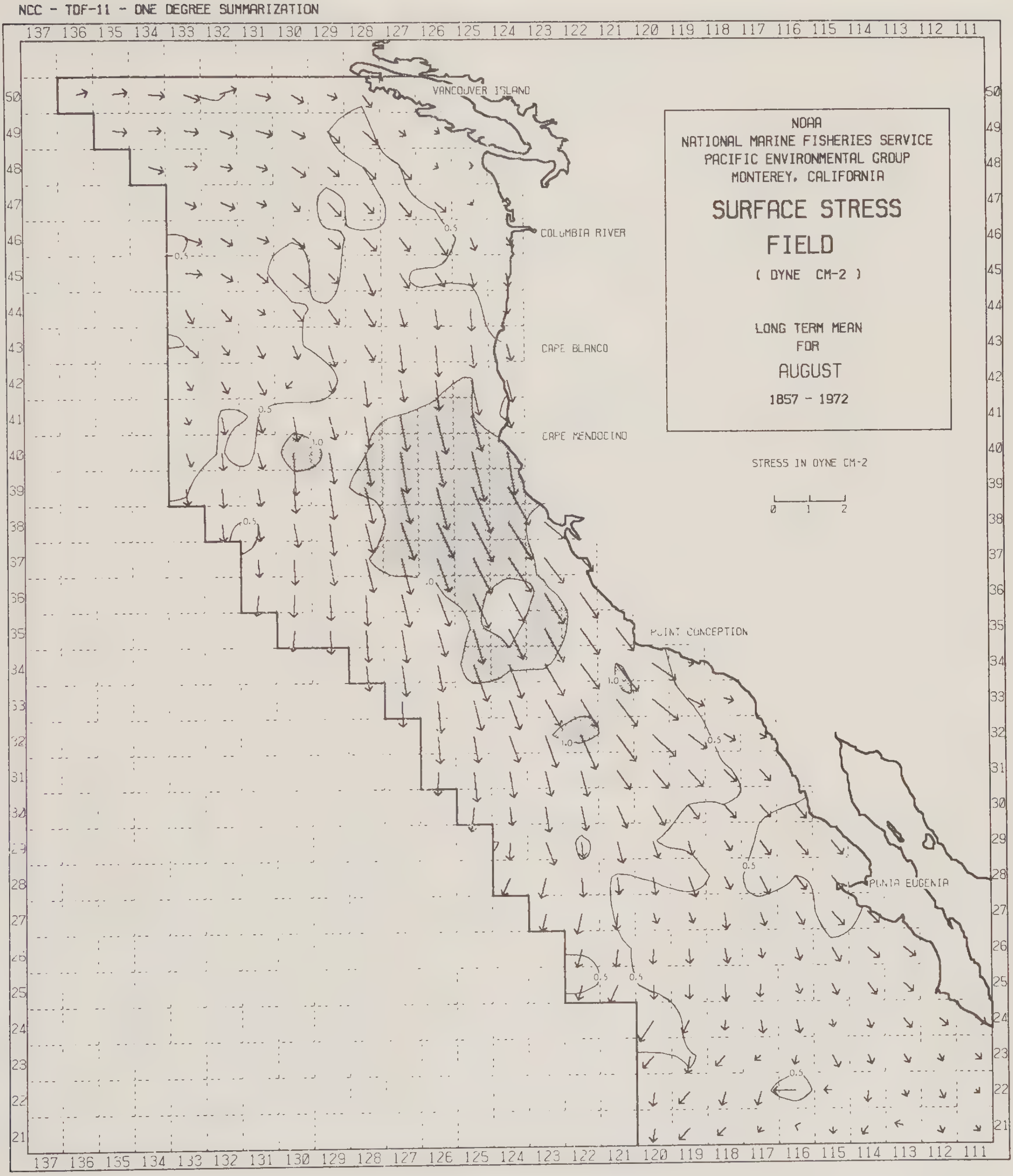

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
SURFACE STRESS FIELD
(DYNE CM-2)
LONG TERM MEAN FOR AUGUST
1857 - 1972
STRESS IN DYNE CM-2
0
1
2
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
0.5
1.0
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21

Chart 8.—Resultant surface wind stress vectors for August.

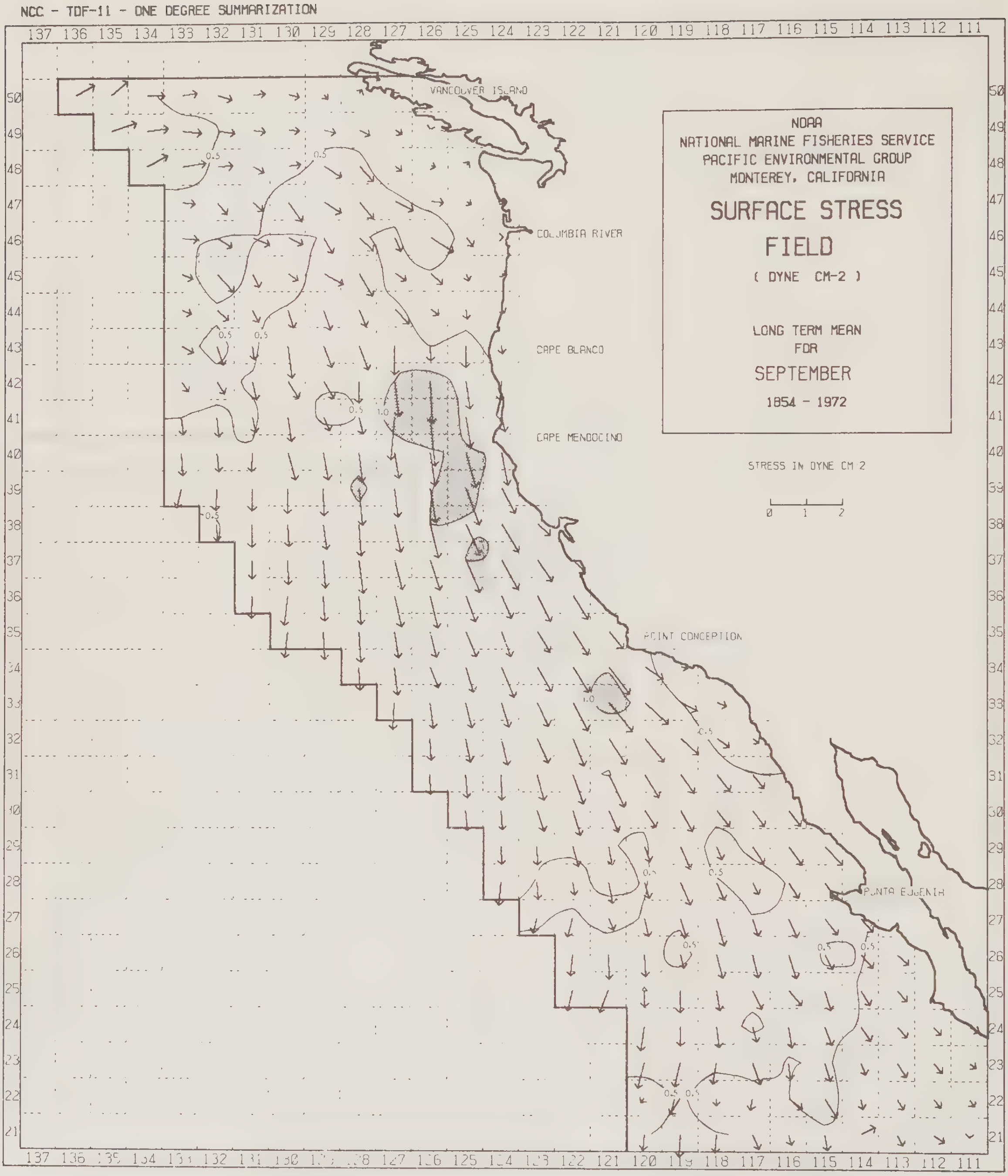
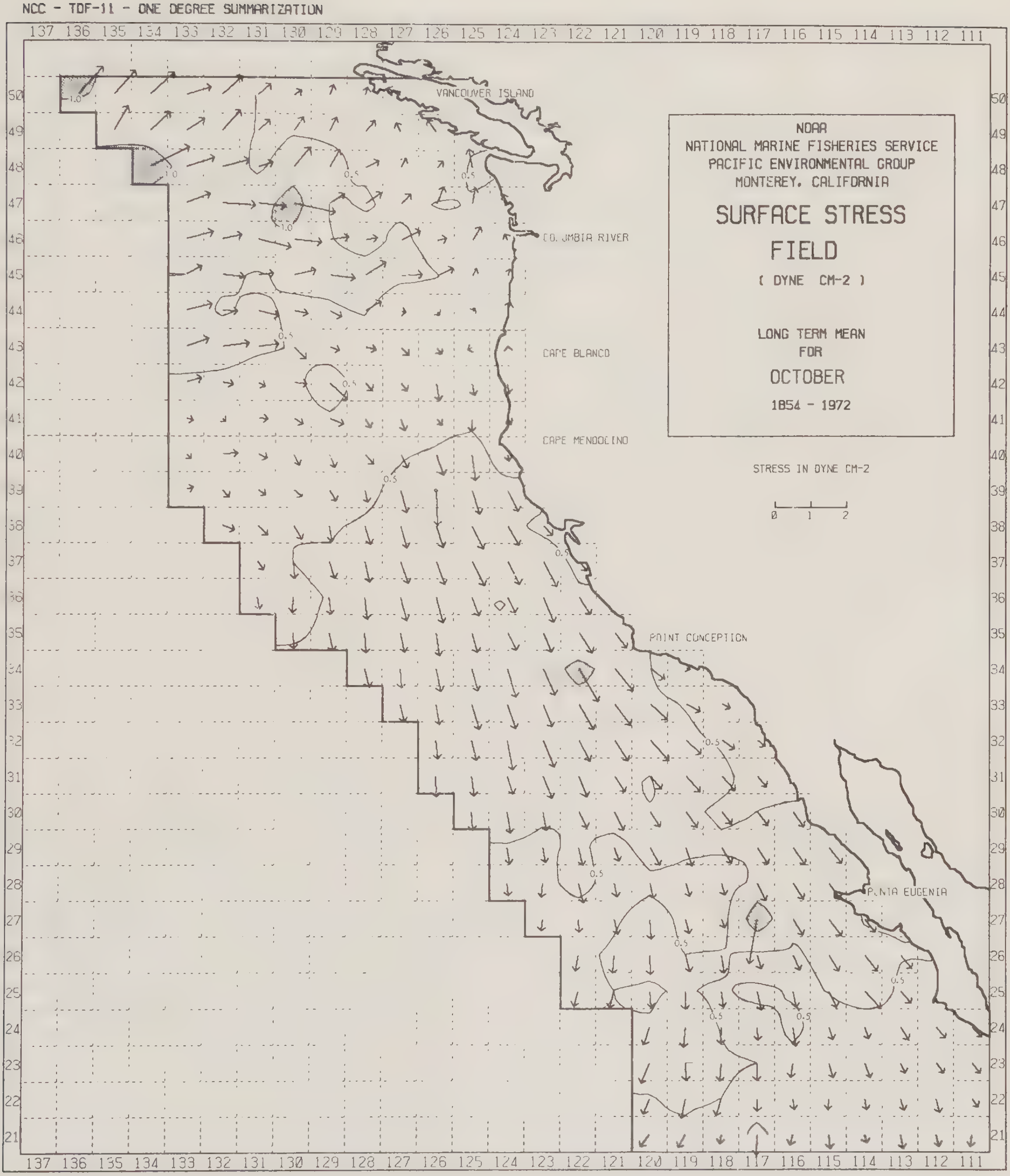

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
SURFACE STRESS
FIELD
(DYNE CM-2)
LONG TERM MEAN
FOR
SEPTEMBER
1854 - 1972
STRESS IN DYNE CM 2
0 1 2
0.5
1.0

Chart 9.—Resultant surface wind stress vectors for September.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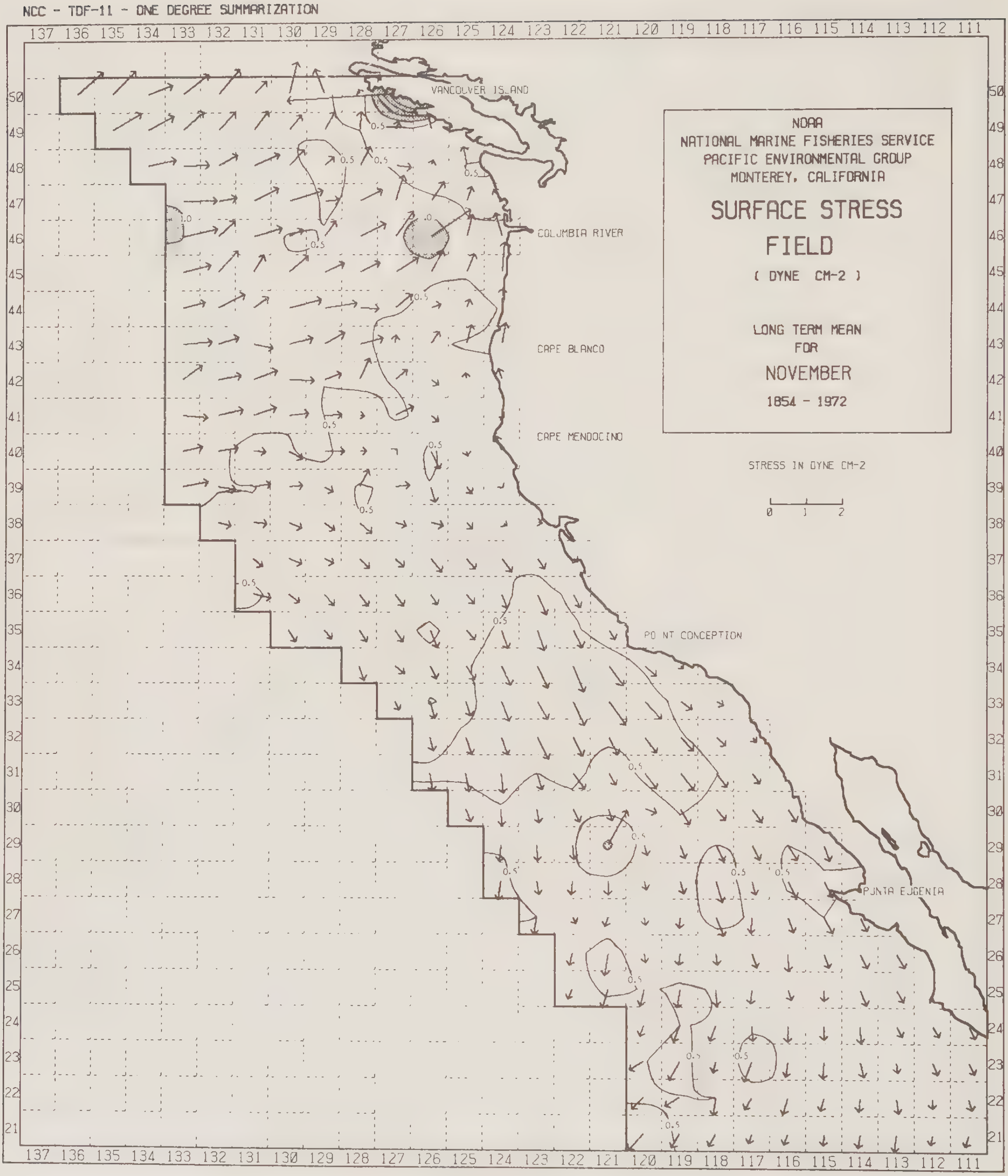
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
SURFACE STRESS FIELD
(DYNE CM-2)
LONG TERM MEAN FOR
OCTOBER
1854 - 1972
STRESS IN DYNE CM-2
0 1 2
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
1.0
0.5

Chart 10.—Resultant surface wind stress vectors for October.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NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
SURFACE STRESS FIELD
(DYNE CM-2)
LONG TERM MEAN FOR
NOVEMBER
1854 - 1972
STRESS IN DYNE CM-2
0 1 2
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
0.5
1.0

Chart 11.—Resultant surface wind stress vectors for November.

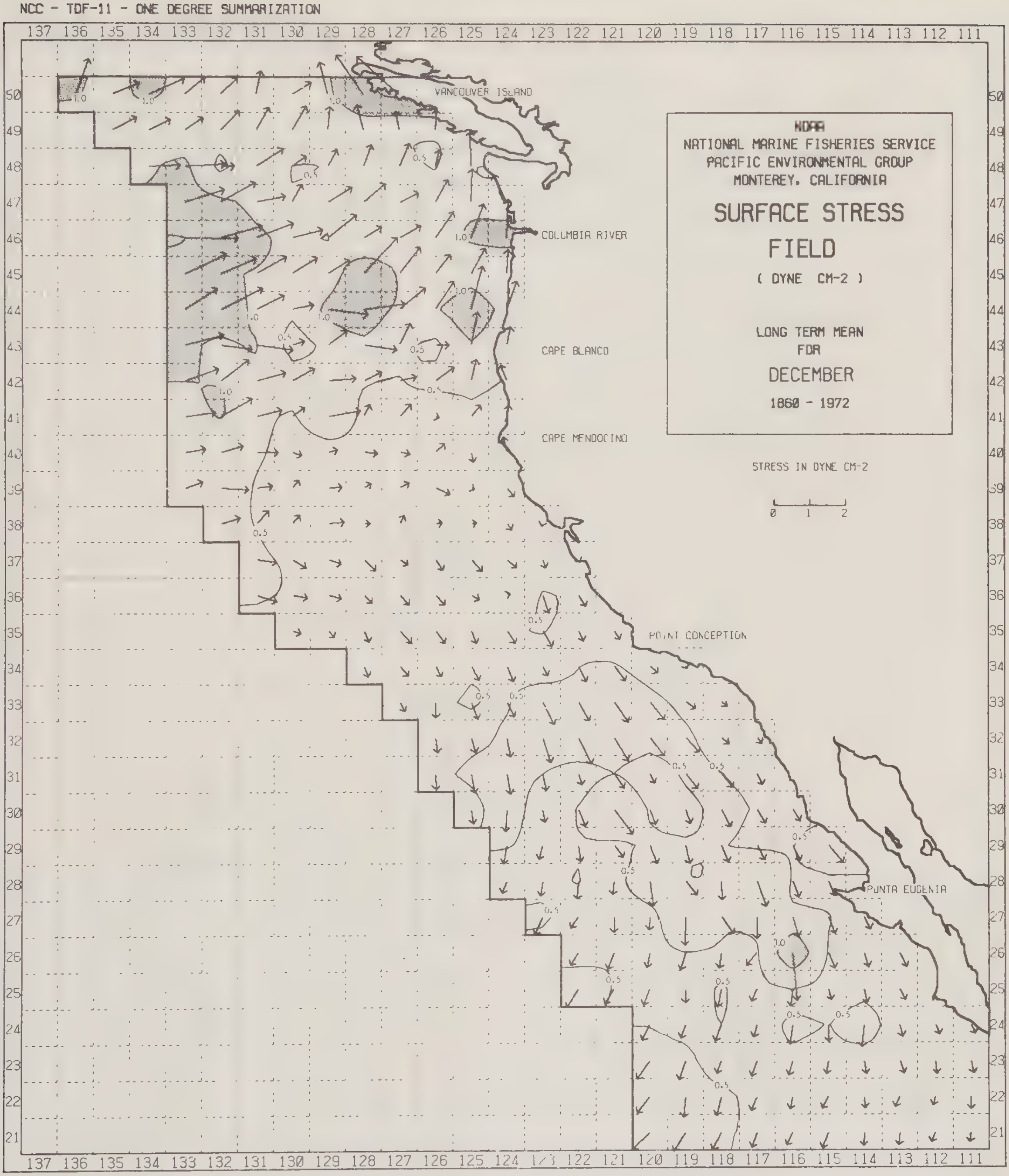

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
SURFACE STRESS
FIELD
(DYNE CM-2)
LONG TERM MEAN
FOR
DECEMBER
1860 - 1972
STRESS IN DYNE CM-2
0 1 2
1.0
0.5

Chart 12.—Resultant surface wind stress vectors for December.

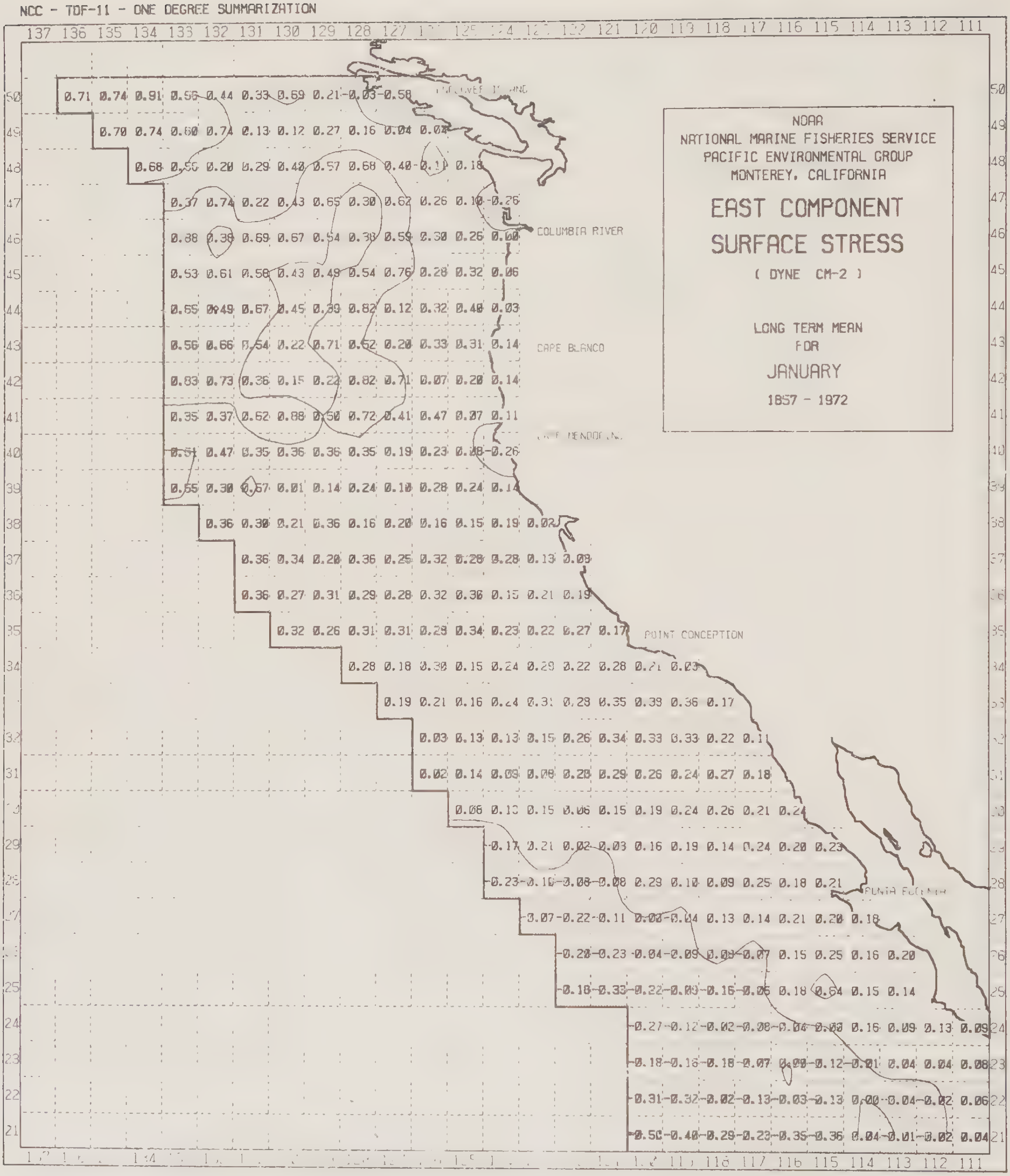

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
EAST COMPONENT
SURFACE STRESS
(DYNE CM-2)
LONG TERM MEAN
FOR
JANUARY
1857 - 1972
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
0.71 0.74 0.91 0.56 0.44 0.33 0.69 0.21 -0.03 -0.58
0.70 0.74 0.60 0.74 0.13 0.12 0.27 0.16 0.04 0.04
0.68 0.55 0.20 0.29 0.40 0.57 0.68 0.40 -0.10 0.18
0.37 0.74 0.22 0.43 0.65 0.30 0.62 0.26 0.10 -0.26
0.38 0.36 0.69 0.67 0.54 0.30 0.59 0.30 0.26 0.00
0.53 0.61 0.58 0.43 0.49 0.54 0.76 0.28 0.32 0.06
0.65 0.49 0.67 0.45 0.39 0.82 0.12 0.32 0.40 0.03
0.56 0.66 0.54 0.22 0.71 0.62 0.20 0.33 0.31 0.14
0.83 0.73 0.36 0.15 0.22 0.82 0.71 0.07 0.20 0.14
0.35 0.37 0.62 0.88 0.50 0.72 0.41 0.47 0.07 0.11
0.54 0.47 0.35 0.36 0.36 0.35 0.19 0.23 0.08 -0.26
0.55 0.30 0.57 0.01 0.14 0.24 0.10 0.28 0.24 0.14
0.36 0.30 0.21 0.36 0.16 0.20 0.16 0.15 0.19 0.02
0.36 0.34 0.20 0.36 0.25 0.32 0.28 0.28 0.13 0.09
0.36 0.27 0.31 0.29 0.28 0.32 0.36 0.15 0.21 0.19
0.32 0.26 0.31 0.31 0.28 0.34 0.23 0.22 0.27 0.17
0.28 0.18 0.30 0.15 0.24 0.29 0.22 0.28 0.21 0.03
0.19 0.21 0.16 0.24 0.31 0.29 0.35 0.39 0.36 0.17
0.03 0.13 0.13 0.15 0.26 0.34 0.33 0.33 0.22 0.11
0.02 0.14 0.09 0.08 0.20 0.29 0.26 0.24 0.27 0.18
0.06 0.10 0.15 0.06 0.15 0.19 0.24 0.26 0.21 0.24
-0.17 0.21 0.02 -0.03 0.16 0.19 0.14 0.24 0.20 0.23
-0.23 -0.10 -0.08 -0.08 0.29 0.10 0.09 0.25 0.18 0.21
-0.07 -0.22 -0.11 0.00 -0.04 0.13 0.14 0.21 0.20 0.18
-0.20 -0.23 -0.04 -0.09 0.09 -0.07 0.15 0.25 0.16 0.20
-0.18 -0.33 -0.22 -0.09 -0.16 -0.05 0.18 0.54 0.15 0.14
-0.27 -0.12 -0.02 -0.08 -0.04 0.00 0.16 0.09 0.13 0.09
-0.18 -0.16 -0.18 -0.07 0.00 -0.12 -0.01 0.04 0.04 0.08
-0.31 -0.32 -0.02 -0.13 -0.03 -0.13 0.00 -0.04 -0.02 0.06
-0.50 -0.40 -0.29 -0.23 -0.35 -0.36 0.04 -0.01 -0.02 0.04

Chart 13.—East component surface wind stress for January.

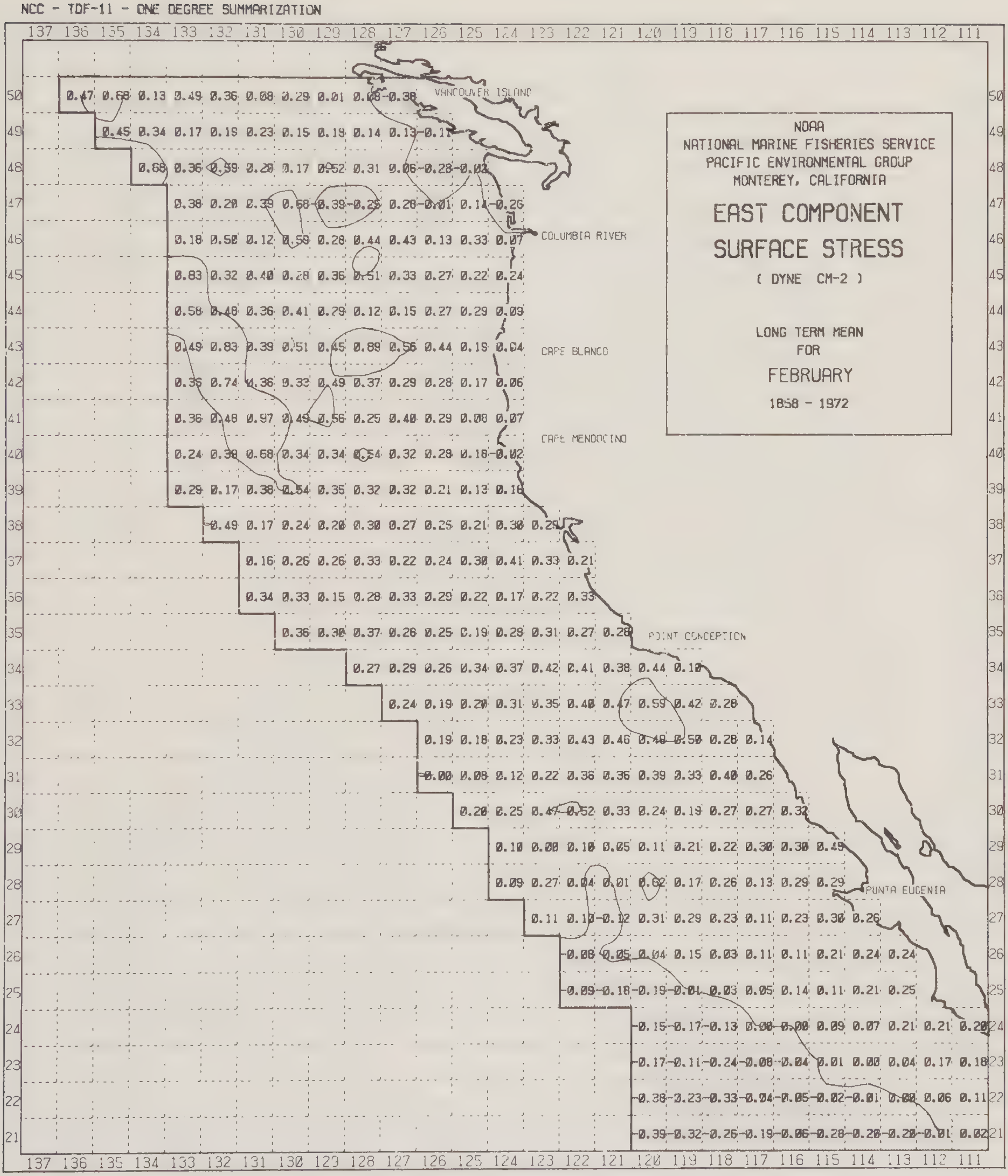

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
EAST COMPONENT
SURFACE STRESS
(DYNE CM-2)
LONG TERM MEAN
FOR
FEBRUARY
1850 - 1972
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
50 0.47 0.68 0.13 0.49 0.36 0.08 0.29 0.01 0.08 -0.38
49 0.45 0.34 0.17 0.19 0.23 0.15 0.19 0.14 0.13 -0.11
48 0.68 0.36 0.59 0.20 0.17 0.52 0.31 0.06 -0.28 -0.02
47 0.38 0.20 0.39 0.68 -0.39 -0.25 0.20 -0.01 0.14 -0.26
46 0.18 0.50 0.12 0.59 0.28 0.44 0.43 0.13 0.33 0.07
45 0.83 0.32 0.40 0.28 0.36 0.51 0.33 0.27 0.22 0.24
44 0.58 0.48 0.36 0.41 0.29 0.12 0.15 0.27 0.29 0.09
43 0.49 0.83 0.39 0.51 0.45 0.89 0.56 0.44 0.19 0.04
42 0.36 0.74 0.36 0.33 0.49 0.37 0.29 0.28 0.17 0.06
41 0.36 0.48 0.97 0.49 0.56 0.25 0.40 0.29 0.08 0.07
40 0.24 0.38 0.68 0.34 0.34 0.54 0.32 0.28 0.18 -0.02
39 0.29 0.17 0.38 0.54 0.35 0.32 0.32 0.21 0.13 0.16
38 -0.49 0.17 0.24 0.20 0.30 0.27 0.25 0.21 0.30 0.29
37 0.16 0.26 0.26 0.33 0.22 0.24 0.30 0.41 0.33 0.21
36 0.34 0.33 0.15 0.28 0.33 0.29 0.22 0.17 0.22 0.33
35 0.36 0.30 0.37 0.26 0.25 0.19 0.29 0.31 0.27 0.28
34 0.27 0.29 0.26 0.34 0.37 0.42 0.41 0.38 0.44 0.10
33 0.24 0.19 0.20 0.31 0.35 0.40 0.47 0.59 0.42 0.28
32 0.19 0.18 0.23 0.33 0.43 0.46 0.40 0.50 0.28 0.14
31 -0.00 0.08 0.12 0.22 0.36 0.36 0.39 0.33 0.40 0.26
30 0.20 0.25 0.47 0.52 0.33 0.24 0.19 0.27 0.27 0.32
29 0.10 0.00 0.10 0.05 0.11 0.21 0.22 0.30 0.30 0.49
28 0.09 0.27 0.04 0.01 0.62 0.17 0.26 0.13 0.29 0.29
27 0.11 0.10 -0.12 0.31 0.29 0.23 0.11 0.23 0.30 0.26
26 -0.08 0.05 0.04 0.15 0.03 0.11 0.11 0.21 0.24 0.24
25 -0.09 -0.18 -0.19 -0.01 0.03 0.05 0.14 0.11 0.21 0.25
24 -0.15 -0.17 -0.13 0.00 -0.00 0.09 0.07 0.21 0.21 0.20
23 -0.17 -0.11 -0.24 -0.08 -0.04 0.01 0.00 0.04 0.17 0.18
22 -0.38 -0.23 -0.33 -0.04 -0.05 -0.02 -0.01 0.00 0.06 0.11
21 -0.39 -0.32 -0.26 -0.19 -0.06 -0.28 -0.20 -0.20 -0.01 0.02

Chart 14.—East component surface wind stress for February.

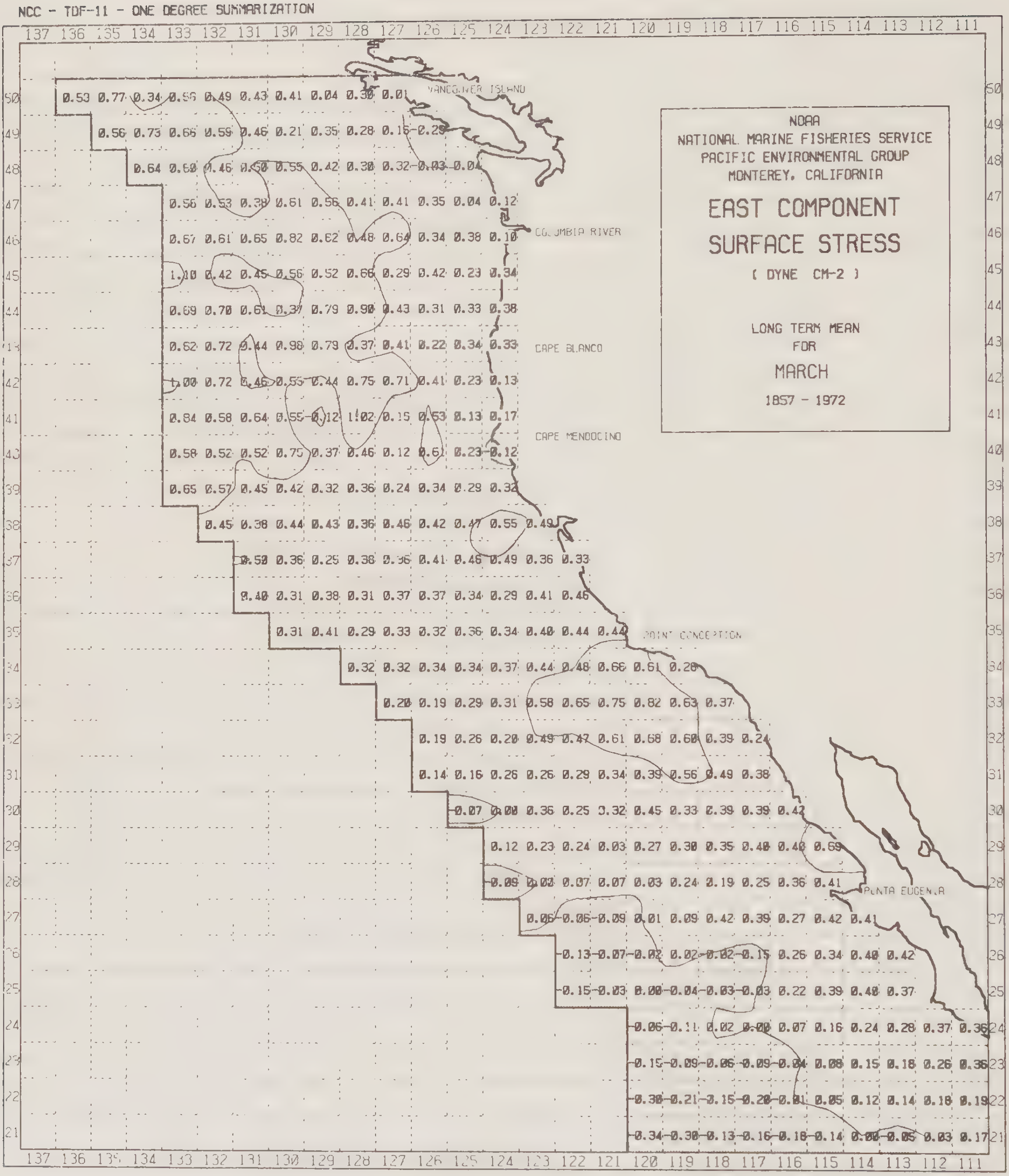
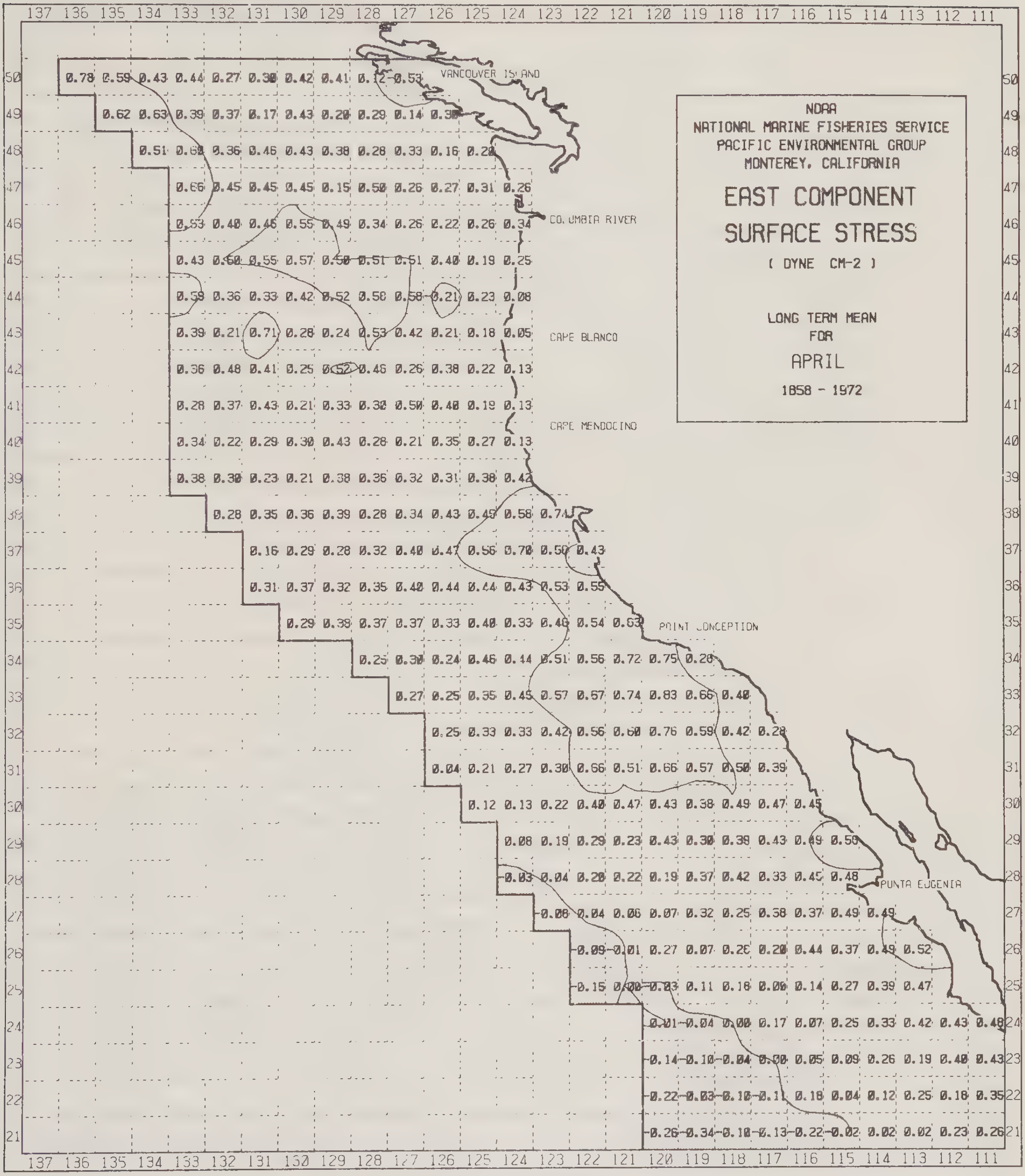

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
EAST COMPONENT
SURFACE STRESS
(DYNE CM-2)
LONG TERM MEAN
FOR
MARCH
1857 - 1972
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
0.53 0.77 0.34 0.56 0.49 0.43 0.41 0.04 0.30 0.01
0.56 0.73 0.66 0.59 0.46 0.21 0.35 0.28 0.15 -0.29
0.64 0.60 0.46 0.50 0.55 0.42 0.30 0.32 -0.03 0.04
0.56 0.53 0.38 0.61 0.56 0.41 0.41 0.35 0.04 0.12
0.67 0.61 0.65 0.82 0.62 0.48 0.64 0.34 0.38 0.10
1.10 0.42 0.45 0.56 0.52 0.66 0.29 0.42 0.23 0.34
0.69 0.70 0.61 0.37 0.79 0.90 0.43 0.31 0.33 0.38
0.62 0.72 0.44 0.98 0.79 0.37 0.41 0.22 0.34 0.33
1.00 0.72 0.46 0.55 0.44 0.75 0.71 0.41 0.23 0.13
0.84 0.58 0.64 0.55 -0.12 1.02 0.15 0.53 0.13 0.17
0.58 0.52 0.52 0.75 0.37 0.46 0.12 0.61 0.23 -0.12
0.65 0.57 0.45 0.42 0.32 0.36 0.24 0.34 0.29 0.32
0.45 0.38 0.44 0.43 0.36 0.46 0.42 0.47 0.55 0.49
0.50 0.36 0.25 0.38 0.36 0.41 0.46 0.49 0.36 0.33
0.40 0.31 0.38 0.31 0.37 0.37 0.34 0.29 0.41 0.46
0.31 0.41 0.29 0.33 0.32 0.36 0.34 0.40 0.44 0.44
0.32 0.32 0.34 0.34 0.37 0.44 0.48 0.66 0.61 0.20
0.20 0.19 0.29 0.31 0.58 0.65 0.75 0.82 0.63 0.37
0.19 0.26 0.20 0.49 0.47 0.61 0.68 0.60 0.39 0.24
0.14 0.16 0.26 0.26 0.29 0.34 0.39 0.56 0.49 0.38
-0.07 0.00 0.36 0.25 0.32 0.45 0.33 0.39 0.39 0.42
0.12 0.23 0.24 0.03 0.27 0.30 0.35 0.40 0.40 0.69
-0.09 0.02 0.07 0.07 0.03 0.24 0.19 0.25 0.36 0.41
0.06 -0.06 -0.09 0.01 0.09 0.42 0.39 0.27 0.42 0.41
-0.13 -0.07 -0.02 0.02 -0.02 -0.15 0.26 0.34 0.40 0.42
-0.15 -0.03 0.00 -0.04 -0.03 -0.03 0.22 0.39 0.40 0.37
-0.06 -0.11 0.02 0.00 0.07 0.16 0.24 0.28 0.37 0.36
-0.15 -0.09 -0.06 -0.09 -0.04 0.08 0.15 0.18 0.26 0.36
-0.30 -0.21 -0.15 -0.20 -0.01 0.05 0.12 0.14 0.18 0.19
-0.34 -0.30 -0.13 -0.16 -0.18 -0.14 0.00 -0.05 0.03 0.17

Chart 15.—East component surface wind stress for March.

NCC - TDF-11 - ONE DEGREE SUMMARIZATION



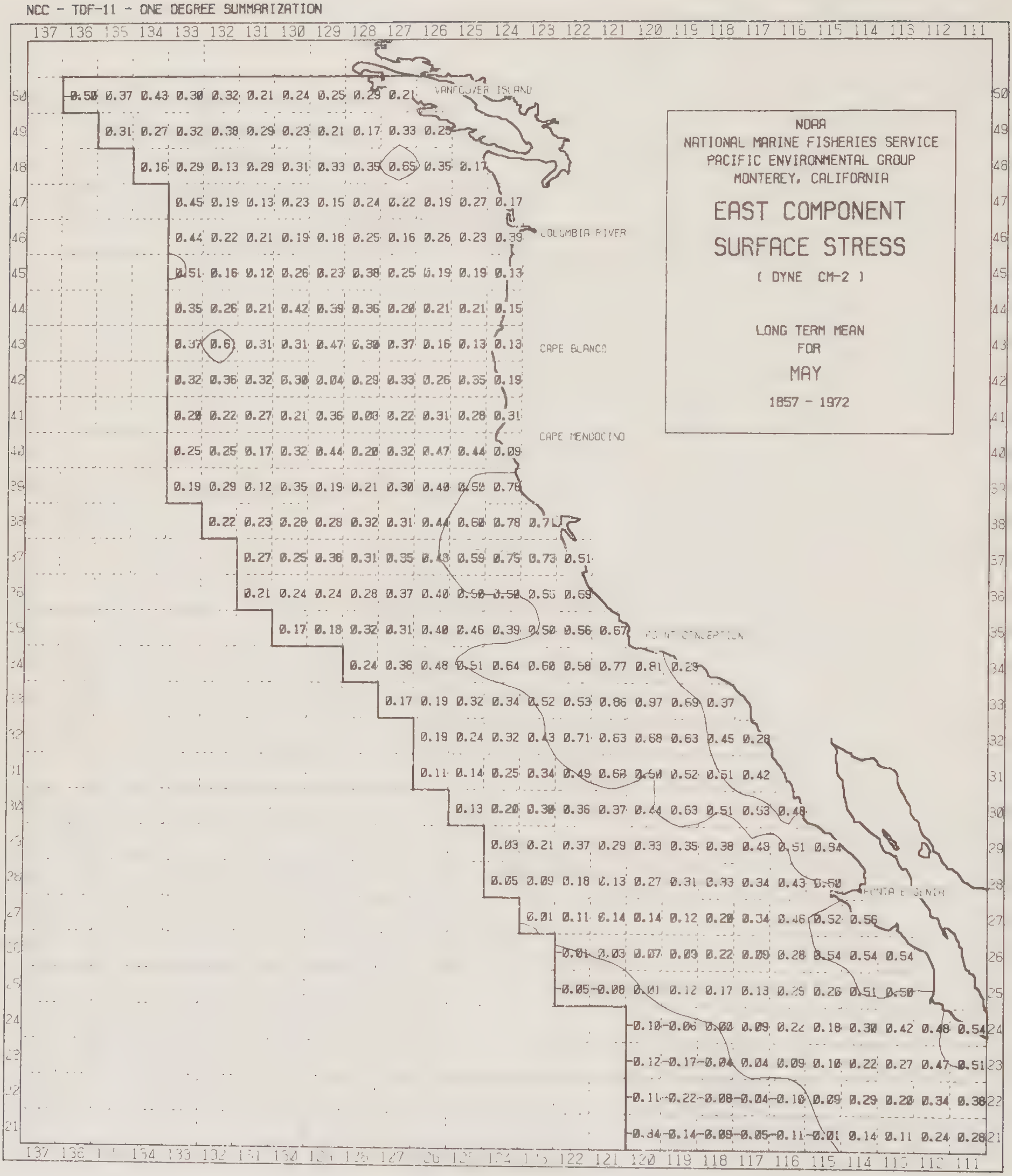
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA

EAST COMPONENT
SURFACE STRESS
(DYNE CM-2)

LONG TERM MEAN
FOR
APRIL
1858 - 1972

	136	135	134	133	132	131	130	129	128	127	126	125	124	123	122	121	120	119	118	117	116	115	114	113	112	111
50	0.78	0.59	0.43	0.44	0.27	0.30	0.42	0.41	0.12	0.53																
49		0.62	0.63	0.39	0.37	0.17	0.43	0.20	0.29	0.14	0.30															
48			0.51	0.60	0.36	0.46	0.43	0.38	0.28	0.33	0.16	0.20														
47				0.66	0.45	0.45	0.45	0.15	0.50	0.26	0.27	0.31	0.26													
46				0.53	0.40	0.46	0.55	0.49	0.34	0.26	0.22	0.26	0.34													
45				0.43	0.60	0.55	0.57	0.50	0.51	0.51	0.40	0.19	0.25													
44				0.59	0.36	0.33	0.42	0.52	0.58	0.58	0.21	0.23	0.08													
43				0.39	0.21	0.71	0.28	0.24	0.53	0.42	0.21	0.18	0.05													
42				0.36	0.48	0.41	0.25	0.52	0.46	0.26	0.38	0.22	0.13													
41				0.28	0.37	0.43	0.21	0.33	0.30	0.50	0.40	0.19	0.13													
40				0.34	0.22	0.29	0.30	0.43	0.28	0.21	0.35	0.27	0.13													
39				0.38	0.30	0.23	0.21	0.38	0.36	0.32	0.31	0.38	0.42													
38					0.28	0.35	0.36	0.39	0.28	0.34	0.43	0.45	0.58	0.74												
37						0.16	0.29	0.28	0.32	0.40	0.47	0.56	0.70	0.50	0.43											
36						0.31	0.37	0.32	0.35	0.40	0.44	0.44	0.43	0.53	0.55											
35							0.29	0.38	0.37	0.37	0.33	0.40	0.33	0.46	0.54	0.63										
34									0.25	0.30	0.24	0.46	0.44	0.51	0.56	0.72	0.75	0.28								
33										0.27	0.25	0.35	0.45	0.57	0.57	0.74	0.83	0.66	0.40							
32											0.25	0.33	0.33	0.42	0.56	0.60	0.76	0.59	0.42	0.28						
31											0.04	0.21	0.27	0.30	0.66	0.51	0.66	0.57	0.50	0.39						
30												0.12	0.13	0.22	0.40	0.47	0.43	0.38	0.49	0.47	0.45					
29													0.08	0.19	0.29	0.23	0.43	0.30	0.39	0.43	0.49	0.50				
28													-0.03	0.04	0.20	0.22	0.19	0.37	0.42	0.33	0.45	0.48				
27														-0.08	0.04	0.06	0.07	0.32	0.25	0.38	0.37	0.49	0.49			
26															-0.09	-0.01	0.27	0.07	0.26	0.20	0.44	0.37	0.49	0.52		
25															-0.15	0.00	-0.03	0.11	0.18	0.00	0.14	0.27	0.39	0.47		
24																	0.01	-0.04	0.00	0.17	0.07	0.25	0.33	0.42	0.43	0.48
23																	-0.14	-0.10	-0.04	0.00	0.05	0.09	0.26	0.19	0.40	0.43
22																	-0.22	-0.03	-0.10	-0.11	0.18	0.04	0.12	0.25	0.18	0.35
21																	-0.26	-0.34	-0.10	-0.13	-0.22	-0.02	0.02	0.02	0.23	0.26

Chart 16.—East component surface wind stress for April.


NCC - TDF-11 - ONE DEGREE SUMMARIZATION
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
EAST COMPONENT
SURFACE STRESS
(DYNE CM-2)
LONG TERM MEAN
FOR
MAY
1857 - 1972
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA

	136	135	134	133	132	131	130	129	128	127	126	125	124	123	122	121	120	119	118	117	116	115	114	113	112	111
50	-0.50	0.37	0.43	0.30	0.32	0.21	0.24	0.25	0.29	0.21																
49		0.31	0.27	0.32	0.38	0.29	0.23	0.21	0.17	0.33	0.25															
48			0.16	0.29	0.13	0.29	0.31	0.33	0.35	0.65	0.35	0.17														
47				0.45	0.19	0.13	0.23	0.15	0.24	0.22	0.19	0.27	0.17													
46				0.44	0.22	0.21	0.19	0.18	0.25	0.16	0.26	0.23	0.39													
45				0.51	0.16	0.12	0.26	0.23	0.38	0.25	0.19	0.19	0.13													
44				0.35	0.26	0.21	0.42	0.39	0.36	0.20	0.21	0.21	0.15													
43				0.37	0.61	0.31	0.31	0.47	0.30	0.37	0.16	0.13	0.13													
42				0.32	0.36	0.32	0.30	0.04	0.29	0.33	0.26	0.35	0.19													
41				0.20	0.22	0.27	0.21	0.36	0.00	0.22	0.31	0.28	0.31													
40				0.25	0.25	0.17	0.32	0.44	0.20	0.32	0.47	0.44	0.09													
39				0.19	0.29	0.12	0.35	0.19	0.21	0.30	0.40	0.50	0.76													
38					0.22	0.23	0.28	0.28	0.32	0.31	0.44	0.60	0.78	0.71												
37						0.27	0.25	0.38	0.31	0.35	0.43	0.59	0.75	0.73	0.51											
36						0.21	0.24	0.24	0.28	0.37	0.40	0.50	0.50	0.55	0.69											
35							0.17	0.18	0.32	0.31	0.40	0.46	0.39	0.50	0.56	0.67										
34									0.24	0.36	0.48	0.51	0.64	0.60	0.58	0.77	0.81	0.29								
33										0.17	0.19	0.32	0.34	0.52	0.53	0.86	0.97	0.69	0.37							
32											0.19	0.24	0.32	0.43	0.71	0.63	0.68	0.63	0.45	0.28						
31											0.11	0.14	0.25	0.34	0.49	0.60	0.50	0.52	0.51	0.42						
30												0.13	0.20	0.30	0.36	0.37	0.44	0.63	0.51	0.53	0.48					
29													0.03	0.21	0.37	0.29	0.33	0.35	0.38	0.43	0.51	0.54				
28													0.05	0.09	0.18	0.13	0.27	0.31	0.33	0.34	0.43	0.50				
27														0.01	0.11	0.14	0.14	0.12	0.20	0.34	0.46	0.52	0.56			
26															-0.01	0.03	0.07	0.03	0.22	0.09	0.28	0.54	0.54	0.54		
25															-0.05	-0.08	0.01	0.12	0.17	0.13	0.25	0.26	0.51	0.50		
24																	-0.10	-0.06	0.00	0.09	0.22	0.18	0.30	0.42	0.48	0.54
23																	-0.12	-0.17	-0.04	0.04	0.09	0.10	0.22	0.27	0.47	0.51
22																	-0.11	-0.22	-0.08	-0.04	-0.10	0.09	0.29	0.20	0.34	0.38
21																	-0.34	-0.14	-0.09	-0.05	-0.11	-0.01	0.14	0.11	0.24	0.28

Chart 17.—East component surface wind stress for May.

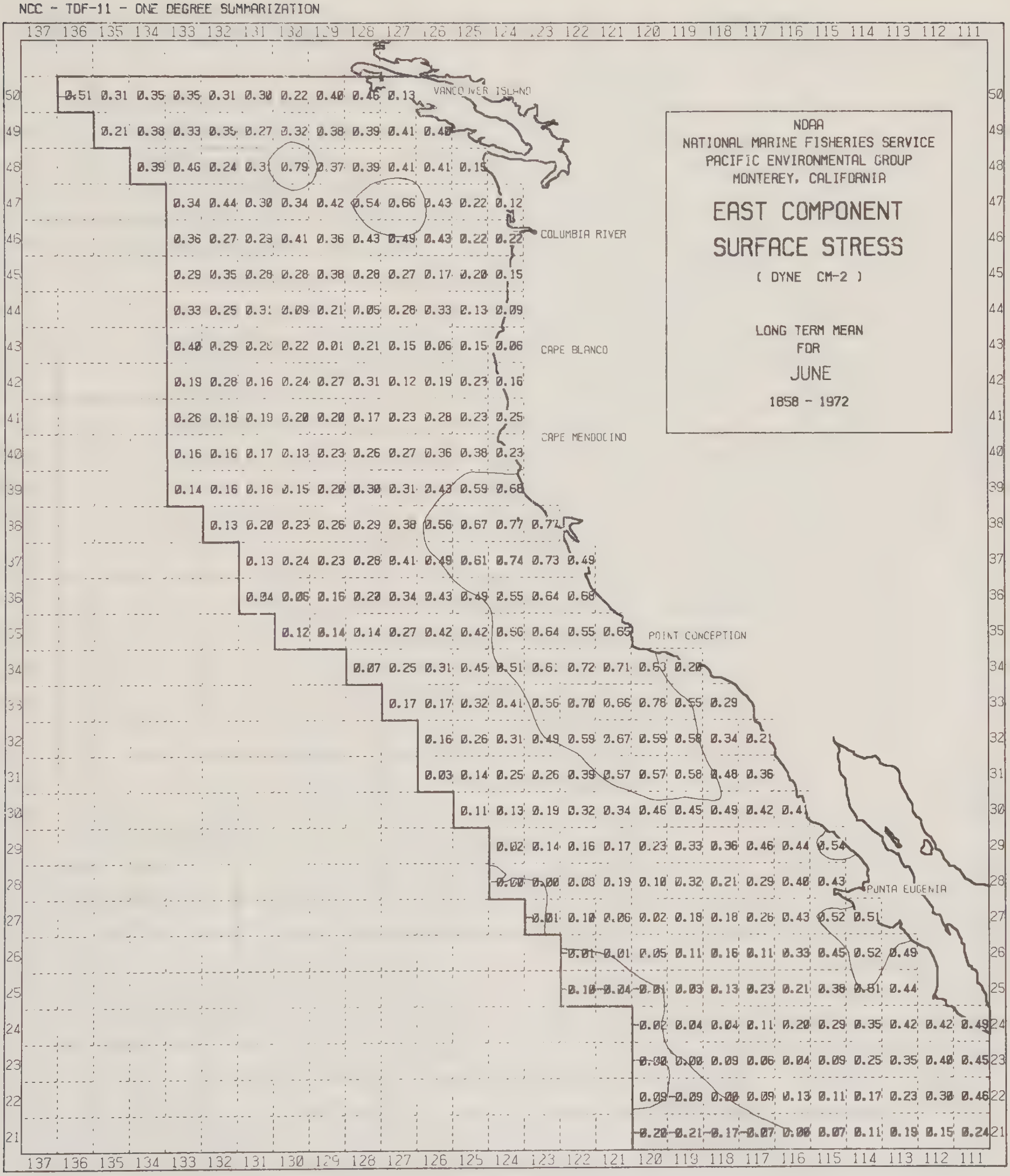

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
EAST COMPONENT
SURFACE STRESS
(DYNE CM-2)
LONG TERM MEAN
FOR
JUNE
1858 - 1972
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA

Chart 18.—East component surface wind stress for June.

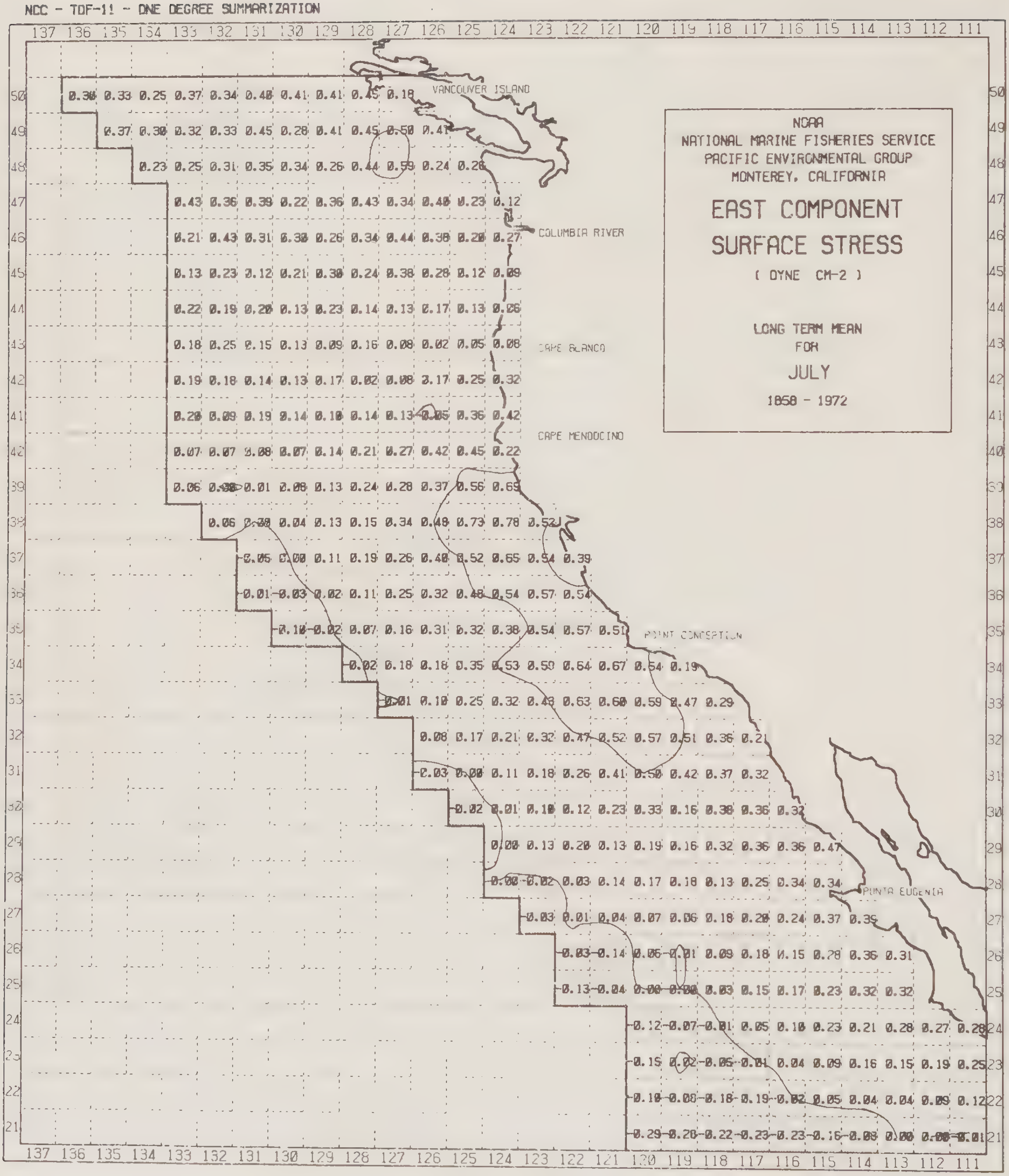

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
EAST COMPONENT
SURFACE STRESS
(DYNE CM-2)
LONG TERM MEAN
FOR
JULY
1858 - 1972
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
0.30 0.33 0.25 0.37 0.34 0.40 0.41 0.41 0.45 0.18
0.37 0.30 0.32 0.33 0.45 0.28 0.41 0.45 0.50 0.41
0.23 0.25 0.31 0.35 0.34 0.26 0.44 0.59 0.24 0.26
0.43 0.36 0.39 0.22 0.36 0.43 0.34 0.40 0.23 0.12
0.21 0.43 0.31 0.30 0.26 0.34 0.44 0.38 0.20 0.27
0.13 0.23 0.12 0.21 0.30 0.24 0.38 0.28 0.12 0.09
0.22 0.19 0.20 0.13 0.23 0.14 0.13 0.17 0.13 0.26
0.18 0.25 0.15 0.13 0.09 0.16 0.08 0.02 0.05 0.08
0.19 0.18 0.14 0.13 0.17 0.02 0.08 0.17 0.25 0.32
0.20 0.09 0.19 0.14 0.10 0.14 0.13 0.05 0.36 0.42
0.07 0.07 0.08 0.07 0.14 0.21 0.27 0.42 0.45 0.22
0.06 0.00 -0.01 0.08 0.13 0.24 0.28 0.37 0.56 0.65
0.06 0.30 0.04 0.13 0.15 0.34 0.48 0.73 0.78 0.52
-0.05 0.00 0.11 0.19 0.26 0.40 0.52 0.65 0.54 0.39
-0.01 -0.03 0.02 0.11 0.25 0.32 0.48 0.54 0.57 0.54
-0.10 -0.02 0.07 0.16 0.31 0.32 0.38 0.54 0.57 0.51
-0.02 0.18 0.16 0.35 0.53 0.50 0.64 0.67 0.54 0.19
-0.01 0.10 0.25 0.32 0.43 0.63 0.60 0.59 0.47 0.29
0.08 0.17 0.21 0.32 0.47 0.52 0.57 0.51 0.36 0.21
-0.03 0.00 0.11 0.18 0.26 0.41 0.50 0.42 0.37 0.32
-0.02 0.01 0.10 0.12 0.23 0.33 0.16 0.38 0.36 0.32
0.00 0.13 0.20 0.13 0.19 0.16 0.32 0.36 0.36 0.47
-0.00 -0.02 0.03 0.14 0.17 0.18 0.13 0.25 0.34 0.34
-0.03 0.01 0.04 0.07 0.06 0.18 0.20 0.24 0.37 0.35
-0.03 -0.14 0.06 -0.01 0.09 0.18 0.15 0.28 0.36 0.31
-0.13 -0.04 0.00 -0.00 0.03 0.15 0.17 0.23 0.32 0.32
-0.12 -0.07 -0.01 0.05 0.10 0.23 0.21 0.28 0.27 0.28
-0.15 0.02 -0.05 -0.01 0.04 0.09 0.16 0.15 0.19 0.25
-0.10 -0.08 -0.18 -0.19 -0.02 0.05 0.04 0.04 0.09 0.12
-0.29 -0.20 -0.22 -0.23 -0.23 -0.16 -0.08 0.00 0.00 -0.01

Chart 19.—East component surface wind stress for July.

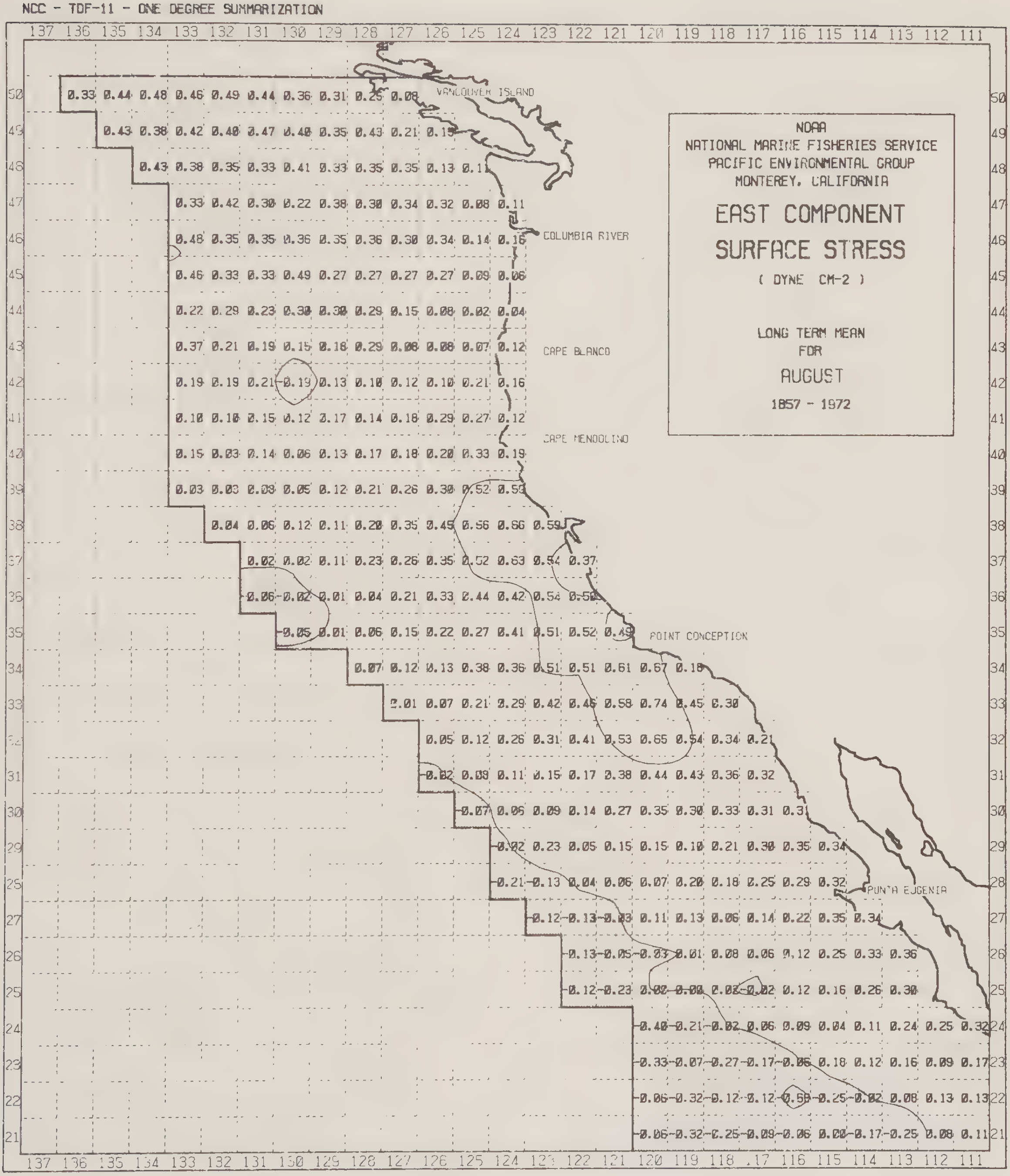

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
EAST COMPONENT
SURFACE STRESS
(DYNE CM-2)
LONG TERM MEAN
FOR
AUGUST
1857 - 1972
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
50 0.33 0.44 0.48 0.46 0.49 0.44 0.36 0.31 0.25 0.08
49 0.43 0.38 0.42 0.40 0.47 0.40 0.35 0.43 0.21 0.15
48 0.43 0.38 0.35 0.33 0.41 0.33 0.35 0.35 0.13 0.11
47 0.33 0.42 0.30 0.22 0.38 0.30 0.34 0.32 0.08 0.11
46 0.48 0.35 0.35 0.36 0.35 0.36 0.30 0.34 0.14 0.16
45 0.46 0.33 0.33 0.49 0.27 0.27 0.27 0.27 0.09 0.06
44 0.22 0.29 0.23 0.30 0.30 0.29 0.15 0.08 0.02 0.04
43 0.37 0.21 0.19 0.15 0.18 0.29 0.08 0.08 0.07 0.12
42 0.19 0.19 0.21 -0.19 0.13 0.10 0.12 0.10 0.21 0.16
41 0.10 0.10 0.15 0.12 0.17 0.14 0.18 0.29 0.27 0.12
40 0.15 0.03 0.14 0.06 0.13 0.17 0.18 0.20 0.33 0.19
39 0.03 0.03 0.08 0.05 0.12 0.21 0.26 0.30 0.52 0.59
38 0.04 0.06 0.12 0.11 0.20 0.35 0.45 0.56 0.66 0.59
37 0.02 0.02 0.11 0.23 0.26 0.35 0.52 0.63 0.54 0.37
36 -0.06 -0.02 0.01 0.04 0.21 0.33 0.44 0.42 0.54 0.50
35 -0.05 0.01 0.06 0.15 0.22 0.27 0.41 0.51 0.52 0.49
34 0.07 0.12 0.13 0.38 0.36 0.51 0.51 0.61 0.67 0.18
33 0.01 0.07 0.21 0.29 0.42 0.46 0.58 0.74 0.45 0.30
32 0.05 0.12 0.26 0.31 0.41 0.53 0.65 0.54 0.34 0.21
31 -0.02 0.03 0.11 0.15 0.17 0.38 0.44 0.43 0.36 0.32
30 -0.07 0.06 0.09 0.14 0.27 0.35 0.30 0.33 0.31 0.31
29 -0.02 0.23 0.05 0.15 0.15 0.10 0.21 0.30 0.35 0.34
28 -0.21 -0.13 0.04 0.06 0.07 0.20 0.18 0.25 0.29 0.32
27 -0.12 -0.13 -0.03 0.11 0.13 0.06 0.14 0.22 0.35 0.34
26 -0.13 -0.05 -0.03 0.01 0.08 0.06 0.12 0.25 0.33 0.36
25 -0.12 -0.23 0.02 -0.00 0.02 -0.02 0.12 0.16 0.26 0.30
24 -0.40 -0.21 -0.02 0.06 0.09 0.04 0.11 0.24 0.25 0.32
23 -0.33 -0.07 -0.27 -0.17 -0.06 0.18 0.12 0.16 0.09 0.17
22 -0.06 -0.32 -0.12 -0.12 -0.58 -0.25 -0.02 0.08 0.13 0.13
21 -0.06 -0.32 -0.25 -0.09 -0.06 0.00 -0.17 -0.25 0.08 0.11
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111

Chart 20.—East component surface wind stress for August.

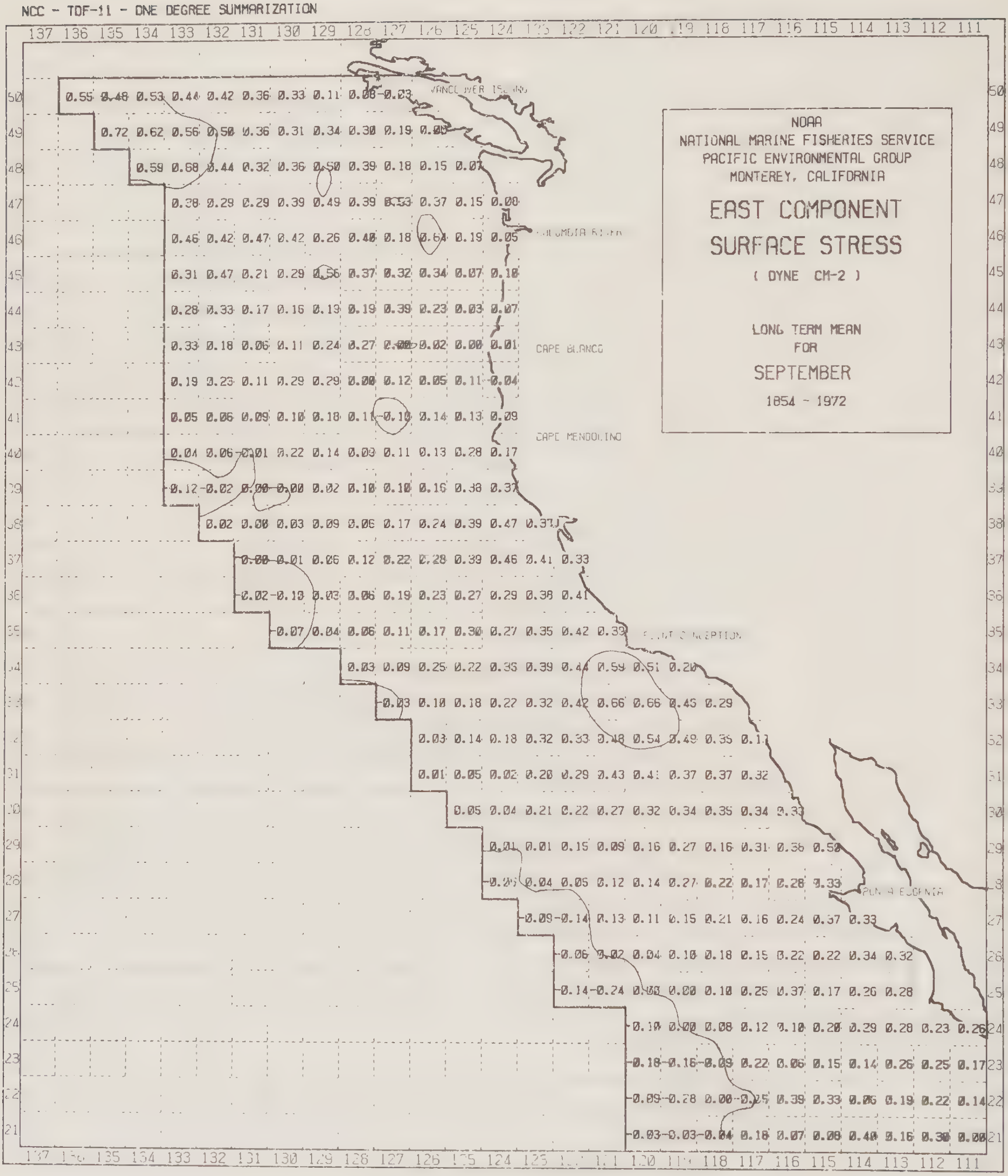

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
EAST COMPONENT
SURFACE STRESS
(DYNE CM-2)
LONG TERM MEAN
FOR
SEPTEMBER
1854 - 1972
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA

Chart 21.—East component surface wind stress for September.

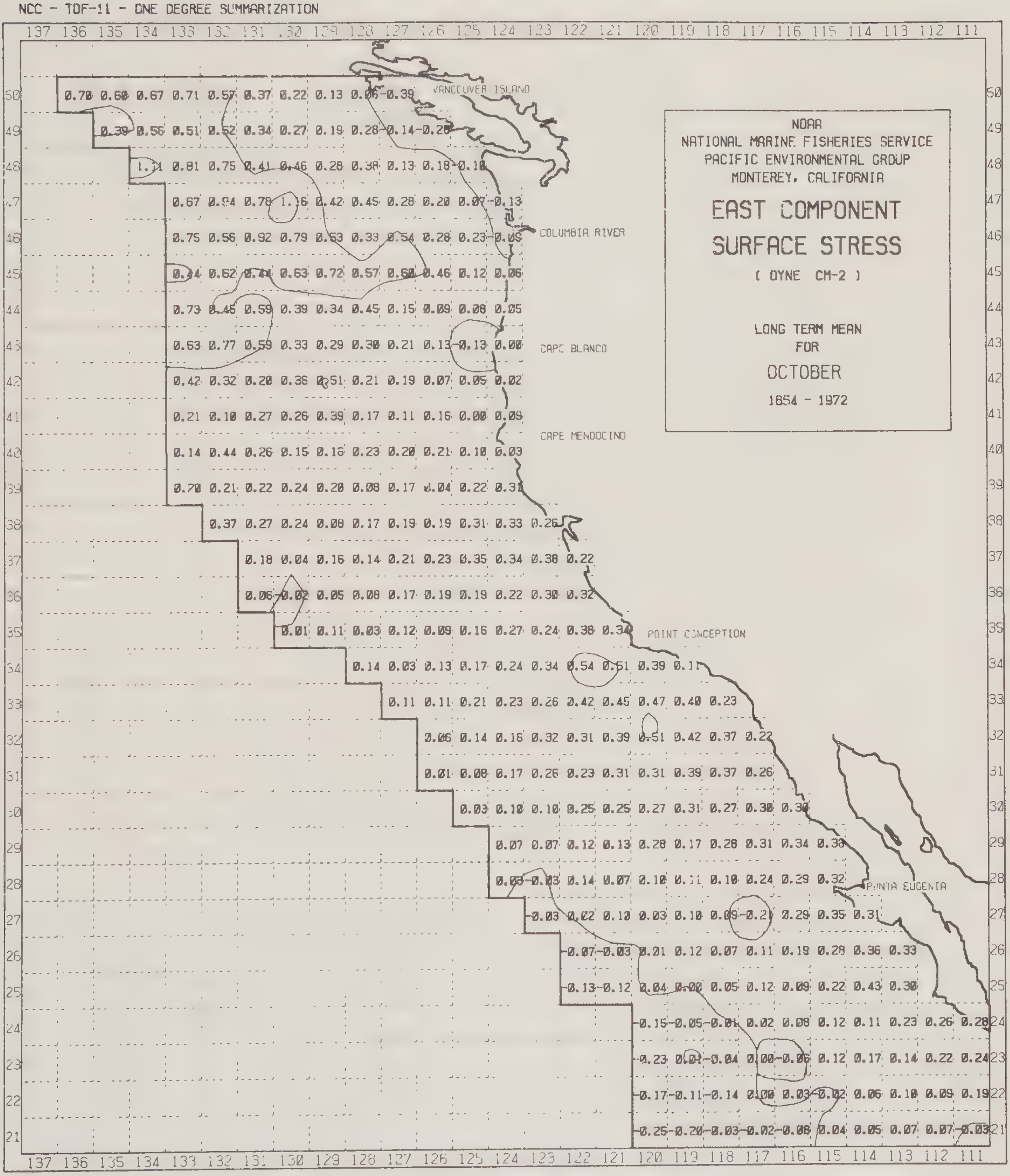

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
EAST COMPONENT
SURFACE STRESS
(DYNE CM-2)
LONG TERM MEAN
FOR
OCTOBER
1854 - 1972
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
0.70 0.60 0.67 0.71 0.57 0.37 0.22 0.13 0.06 -0.39
0.39 0.56 0.51 0.52 0.34 0.27 0.19 0.28 -0.14 -0.20
1.11 0.81 0.75 0.41 0.46 0.28 0.38 0.13 0.18 -0.10
0.67 0.94 0.78 1.16 0.42 0.45 0.28 0.20 0.07 -0.13
0.75 0.56 0.92 0.79 0.63 0.33 0.54 0.28 0.23 -0.09
0.44 0.62 0.44 0.63 0.72 0.57 0.60 0.46 0.12 0.06
0.73 0.45 0.59 0.39 0.34 0.45 0.15 0.09 0.08 0.05
0.63 0.77 0.59 0.33 0.29 0.30 0.21 0.13 -0.13 0.00
0.42 0.32 0.20 0.36 0.51 0.21 0.19 0.07 0.05 0.02
0.21 0.10 0.27 0.26 0.39 0.17 0.11 0.16 0.00 0.09
0.14 0.44 0.26 0.15 0.16 0.23 0.20 0.21 0.10 0.03
0.70 0.21 0.22 0.24 0.20 0.08 0.17 0.04 0.22 0.31
0.37 0.27 0.24 0.08 0.17 0.19 0.19 0.31 0.33 0.26
0.18 0.04 0.16 0.14 0.21 0.23 0.35 0.34 0.38 0.22
0.06 -0.02 0.05 0.08 0.17 0.19 0.19 0.22 0.30 0.32
0.01 0.11 0.03 0.12 0.09 0.16 0.27 0.24 0.38 0.34
0.14 0.03 0.13 0.17 0.24 0.34 0.54 0.51 0.39 0.11
0.11 0.11 0.21 0.23 0.26 0.42 0.45 0.47 0.40 0.23
0.06 0.14 0.16 0.32 0.31 0.39 0.51 0.42 0.37 0.22
0.01 0.08 0.17 0.26 0.23 0.31 0.31 0.39 0.37 0.26
0.03 0.10 0.10 0.25 0.25 0.27 0.31 0.27 0.30 0.30
0.07 0.07 0.12 0.13 0.28 0.17 0.28 0.31 0.34 0.38
0.03 -0.03 0.14 0.07 0.10 0.11 0.10 0.24 0.29 0.32
-0.03 0.02 0.10 0.03 0.10 0.09 -0.21 0.29 0.35 0.31
-0.07 -0.03 0.01 0.12 0.07 0.11 0.19 0.28 0.36 0.33
-0.13 -0.12 0.04 0.00 0.05 0.12 0.09 0.22 0.43 0.30
-0.15 -0.05 -0.01 0.02 0.08 0.12 0.11 0.23 0.26 0.28
-0.23 0.02 -0.04 0.00 -0.06 0.12 0.17 0.14 0.22 0.24
-0.17 -0.11 -0.14 0.00 0.03 -0.02 0.06 0.10 0.09 0.19
-0.25 -0.20 -0.03 -0.02 -0.08 0.04 0.05 0.07 0.07 -0.03

Chart 22.—East component surface wind stress for October.

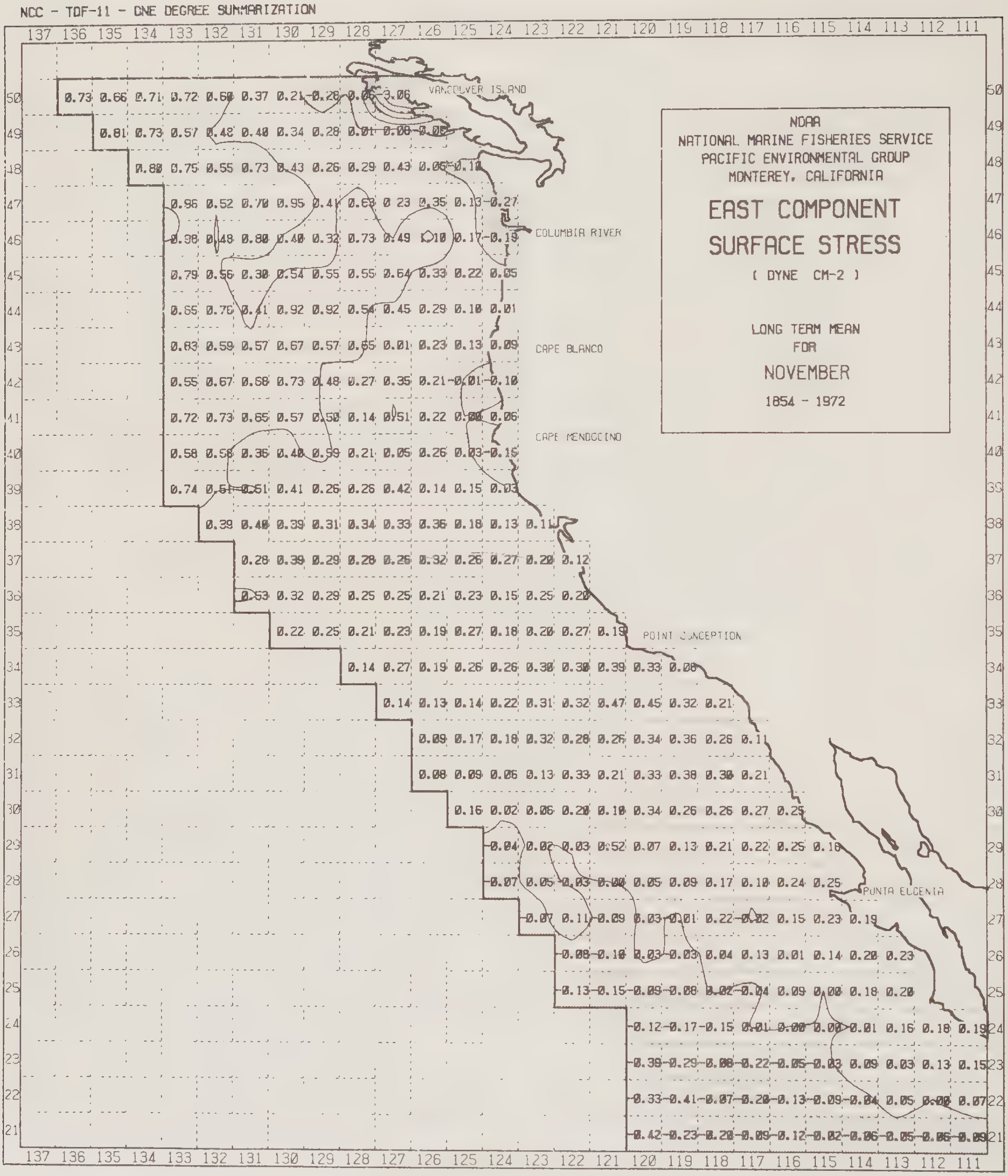

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
EAST COMPONENT
SURFACE STRESS
(DYNE CM-2)
LONG TERM MEAN
FOR
NOVEMBER
1854 - 1972
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
0.73 0.66 0.71 0.72 0.60 0.37 0.21 -0.20 -0.06 -3.06
0.81 0.73 0.57 0.48 0.40 0.34 0.28 0.01 0.00 -0.00
0.80 0.75 0.55 0.73 0.43 0.26 0.29 0.43 0.06 -0.10
0.96 0.52 0.70 0.95 0.41 0.63 0.23 0.35 0.13 -0.27
0.98 0.48 0.80 0.40 0.32 0.73 0.49 0.10 0.17 -0.19
0.79 0.56 0.30 0.54 0.55 0.55 0.64 0.33 0.22 0.05
0.65 0.76 0.41 0.92 0.92 0.54 0.45 0.29 0.10 0.01
0.63 0.59 0.57 0.67 0.57 0.65 0.01 0.23 0.13 0.09
0.55 0.67 0.68 0.73 0.48 0.27 0.35 0.21 -0.01 -0.10
0.72 0.73 0.65 0.57 0.50 0.14 0.51 0.22 0.00 0.06
0.58 0.58 0.36 0.40 0.59 0.21 0.05 0.26 0.03 -0.15
0.74 0.51 0.51 0.41 0.26 0.26 0.42 0.14 0.15 0.03
0.39 0.40 0.39 0.31 0.34 0.33 0.36 0.18 0.13 0.11
0.28 0.39 0.29 0.28 0.25 0.32 0.26 0.27 0.20 0.12
0.53 0.32 0.29 0.25 0.25 0.21 0.23 0.15 0.25 0.20
0.22 0.25 0.21 0.23 0.19 0.27 0.18 0.20 0.27 0.19
0.14 0.27 0.19 0.26 0.26 0.30 0.30 0.39 0.33 0.08
0.14 0.13 0.14 0.22 0.31 0.32 0.47 0.45 0.32 0.21
0.09 0.17 0.18 0.32 0.28 0.26 0.34 0.36 0.26 0.11
0.08 0.09 0.06 0.13 0.33 0.21 0.33 0.38 0.30 0.21
0.16 0.02 0.06 0.20 0.10 0.34 0.26 0.26 0.27 0.25
-0.04 0.02 0.03 0.52 0.07 0.13 0.21 0.22 0.25 0.10
-0.07 0.05 -0.03 -0.00 0.05 0.09 0.17 0.10 0.24 0.25
-0.07 0.11 -0.09 0.03 -0.01 0.22 -0.02 0.15 0.23 0.19
-0.08 -0.10 0.03 -0.03 0.04 0.13 0.01 0.14 0.20 0.23
-0.13 -0.15 -0.09 -0.08 0.02 -0.04 0.09 0.00 0.18 0.20
-0.12 -0.17 -0.15 0.01 0.00 0.00 0.01 0.16 0.18 0.19
-0.39 -0.29 -0.08 -0.22 -0.05 -0.03 0.09 0.03 0.13 0.15
-0.33 -0.41 -0.07 -0.20 -0.13 -0.09 -0.04 0.05 0.00 0.07
-0.42 -0.23 -0.20 -0.09 -0.12 -0.02 -0.06 -0.05 -0.06 -0.09

Chart 23.—East component surface wind stress for November.

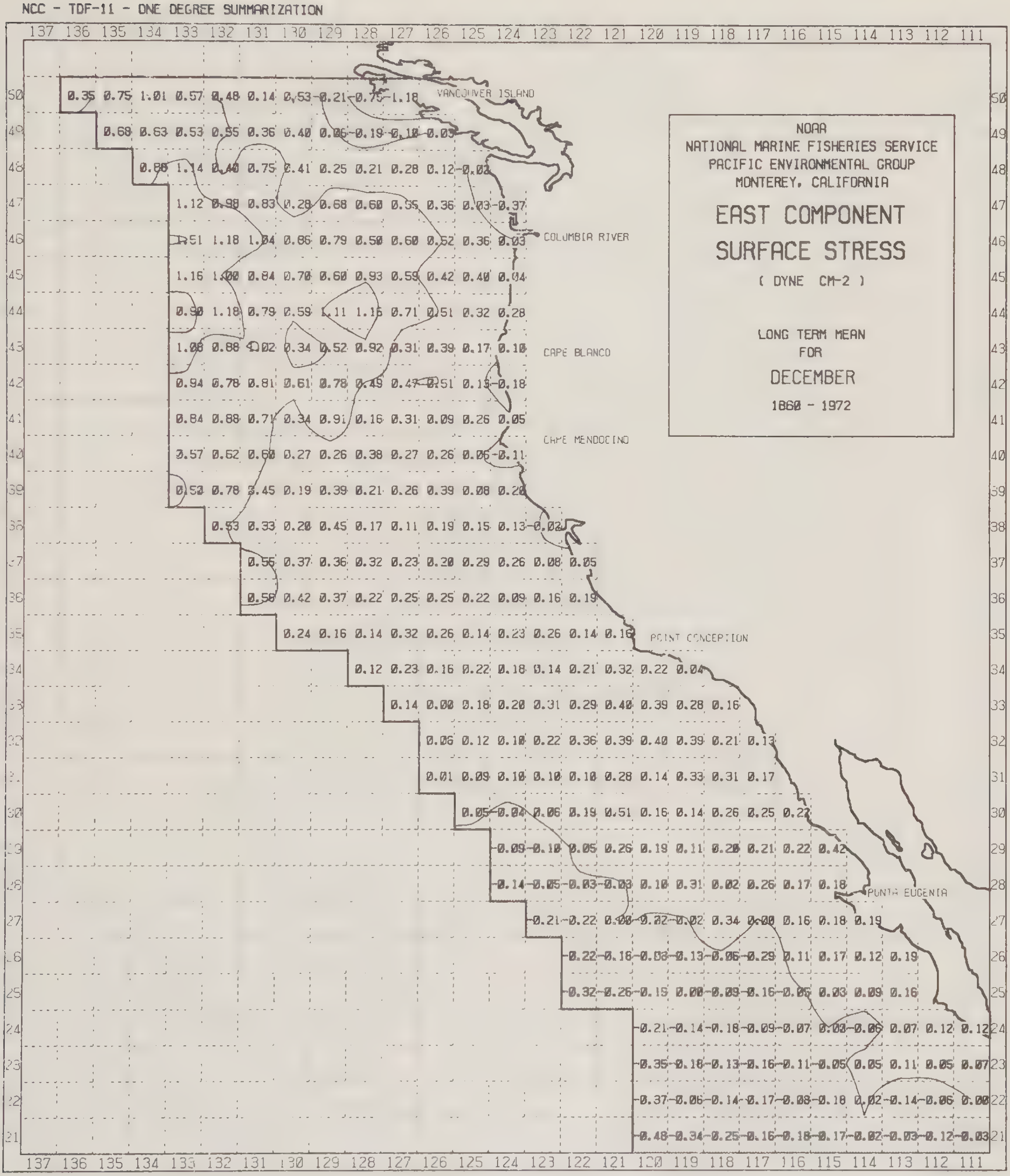

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
EAST COMPONENT
SURFACE STRESS
(DYNE CM-2)
LONG TERM MEAN
FOR
DECEMBER
1860 - 1972
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
0.35 0.75 1.01 0.57 0.48 0.14 0.53 -0.21 -0.75 -1.18
0.68 0.63 0.53 0.55 0.36 0.40 0.06 -0.19 -0.10 -0.03
0.88 1.14 0.40 0.75 0.41 0.25 0.21 0.28 0.12 -0.02
1.12 0.98 0.83 0.28 0.68 0.60 0.55 0.36 0.03 -0.37
1.51 1.18 1.04 0.86 0.79 0.50 0.60 0.52 0.36 0.03
1.16 1.00 0.84 0.70 0.60 0.93 0.59 0.42 0.40 0.04
0.90 1.18 0.79 0.59 1.11 1.16 0.71 0.51 0.32 0.28
1.08 0.88 1.02 0.34 0.52 0.92 0.31 0.39 0.17 0.10
0.94 0.78 0.81 0.61 0.78 0.49 0.47 -0.51 0.13 -0.18
0.84 0.88 0.71 0.34 0.91 0.16 0.31 0.09 0.26 0.05
0.57 0.62 0.60 0.27 0.26 0.38 0.27 0.26 0.06 -0.11
0.52 0.78 0.45 0.19 0.39 0.21 0.26 0.39 0.08 0.20
0.53 0.33 0.20 0.45 0.17 0.11 0.19 0.15 0.13 -0.02
0.55 0.37 0.36 0.32 0.23 0.20 0.29 0.26 0.08 0.05
0.56 0.42 0.37 0.22 0.25 0.25 0.22 0.09 0.16 0.19
0.24 0.16 0.14 0.32 0.26 0.14 0.23 0.26 0.14 0.16
0.12 0.23 0.16 0.22 0.18 0.14 0.21 0.32 0.22 0.04
0.14 0.00 0.18 0.20 0.31 0.29 0.40 0.39 0.28 0.16
0.06 0.12 0.10 0.22 0.36 0.39 0.40 0.39 0.21 0.13
0.01 0.09 0.10 0.10 0.10 0.28 0.14 0.33 0.31 0.17
0.05 -0.04 0.06 0.19 0.51 0.16 0.14 0.26 0.25 0.22
-0.09 -0.10 0.05 0.26 0.19 0.11 0.20 0.21 0.22 0.42
-0.14 -0.05 -0.03 -0.03 0.10 0.31 0.02 0.26 0.17 0.18
-0.21 -0.22 0.00 -0.02 -0.02 0.34 0.00 0.16 0.18 0.19
-0.22 -0.16 -0.03 -0.13 -0.06 -0.29 0.11 0.17 0.12 0.19
-0.32 -0.26 -0.15 0.00 -0.09 -0.16 -0.05 0.03 0.09 0.16
-0.21 -0.14 -0.18 -0.09 -0.07 0.03 -0.06 0.07 0.12 0.12
-0.35 -0.18 -0.13 -0.16 -0.11 -0.05 0.05 0.11 0.05 0.07
-0.37 -0.06 -0.14 -0.17 -0.08 -0.18 0.02 -0.14 -0.06 0.00
-0.48 -0.34 -0.25 -0.16 -0.18 -0.17 -0.02 -0.03 -0.12 -0.03

Chart 24.—East component surface wind stress for December.

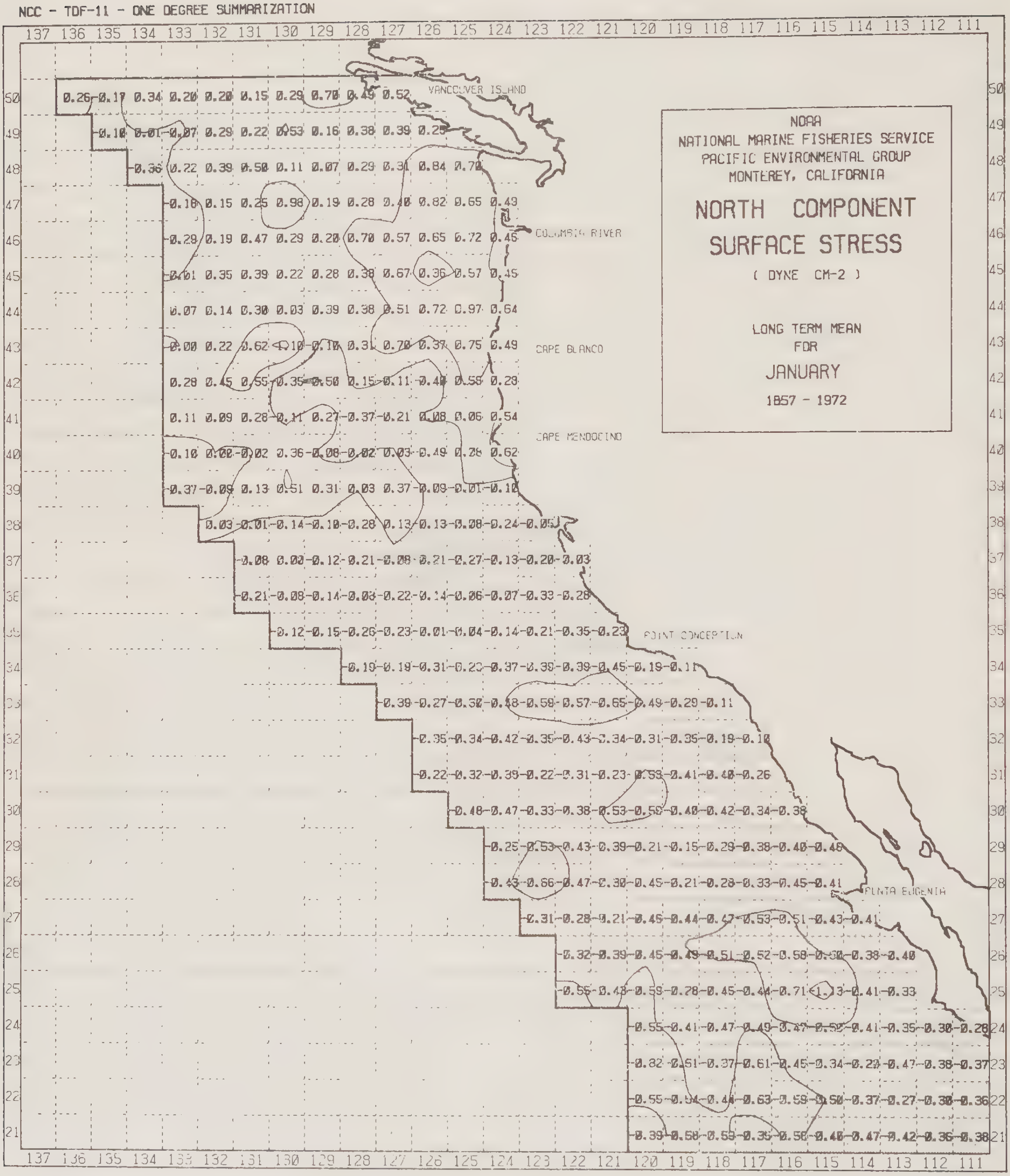

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
NORTH COMPONENT
SURFACE STRESS
(DYNE CM-2)
LONG TERM MEAN
FOR
JANUARY
1857 - 1972
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA

Chart 25.—North component surface wind stress for January.

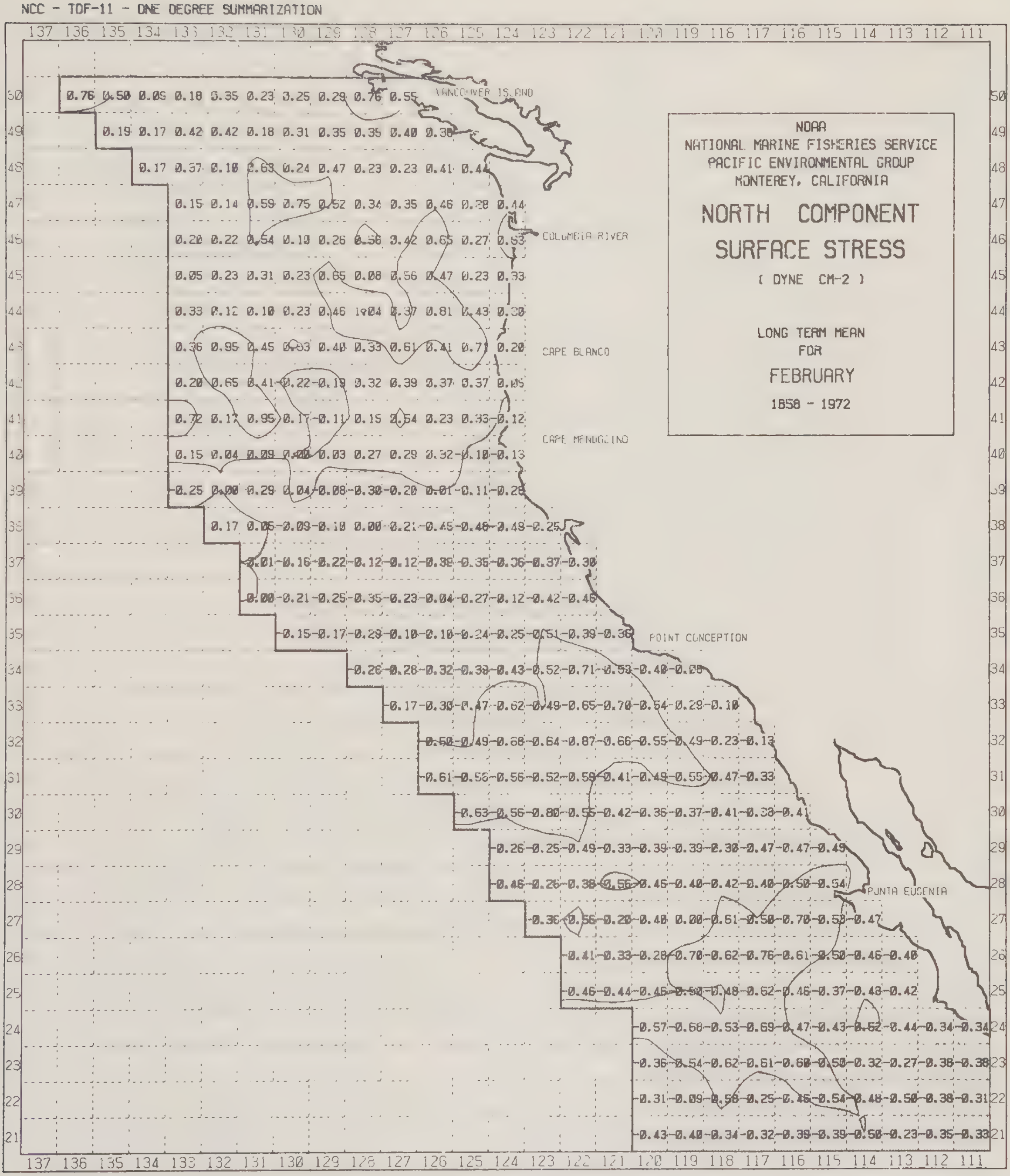

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
NORTH COMPONENT
SURFACE STRESS
(DYNE CM-2)
LONG TERM MEAN
FOR
FEBRUARY
1858 - 1972
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
50 0.76 0.50 0.09 0.18 0.35 0.23 0.25 0.29 0.76 0.55
49 0.19 0.17 0.42 0.42 0.18 0.31 0.35 0.35 0.40 0.38
48 0.17 0.37 0.10 0.63 0.24 0.47 0.23 0.23 0.41 0.44
47 0.15 0.14 0.59 0.75 0.52 0.34 0.35 0.46 0.28 0.44
46 0.20 0.22 0.54 0.10 0.26 0.56 0.42 0.65 0.27 0.63
45 0.05 0.23 0.31 0.23 0.65 0.08 0.56 0.47 0.23 0.33
44 0.33 0.12 0.10 0.23 0.46 1.04 0.37 0.81 0.43 0.30
43 0.36 0.95 0.45 0.53 0.40 0.33 0.61 0.41 0.71 0.20
42 0.20 0.65 0.41-0.22-0.19 0.32 0.39 0.37 0.37 0.05
41 0.72 0.17 0.95 0.17-0.11 0.15 0.54 0.23 0.33-0.12
40 0.15 0.04 0.09 0.00 0.03 0.27 0.29 0.32-0.10-0.13
39 -0.25 0.00 0.29 0.04-0.08-0.30-0.20 0.01-0.11-0.28
38 0.17 0.05-0.09-0.10 0.00-0.21-0.45-0.46-0.49-0.25
37 -0.01-0.16-0.22-0.12-0.12-0.39-0.35-0.36-0.37-0.30
36 -0.00-0.21-0.25-0.35-0.23-0.04-0.27-0.12-0.42-0.46
35 -0.15-0.17-0.29-0.10-0.10-0.24-0.25-0.51-0.39-0.36
34 -0.26-0.28-0.32-0.33-0.43-0.52-0.71-0.53-0.40-0.05
33 -0.17-0.30-0.47-0.62-0.49-0.65-0.70-0.54-0.29-0.10
32 -0.50-0.49-0.68-0.64-0.87-0.66-0.55-0.49-0.23-0.13
31 -0.61-0.56-0.56-0.52-0.59-0.41-0.49-0.55-0.47-0.33
30 -0.63-0.56-0.80-0.55-0.42-0.36-0.37-0.41-0.33-0.41
29 -0.26-0.25-0.49-0.33-0.39-0.39-0.30-0.47-0.47-0.49
28 -0.46-0.26-0.38-0.56-0.46-0.40-0.42-0.40-0.50-0.54
27 -0.36-0.56-0.20-0.40 0.00-0.61-0.50-0.70-0.53-0.47
26 -0.41-0.33-0.28-0.70-0.62-0.76-0.61-0.50-0.46-0.40
25 -0.46-0.44-0.46-0.50-0.48-0.62-0.46-0.37-0.48-0.42
24 -0.57-0.68-0.53-0.69-0.47-0.43-0.52-0.44-0.34-0.34
23 -0.36-0.54-0.62-0.61-0.60-0.50-0.32-0.27-0.38-0.38
22 -0.31-0.09-0.58-0.25-0.46-0.54-0.48-0.50-0.38-0.31
21 -0.43-0.40-0.34-0.32-0.39-0.39-0.50-0.23-0.35-0.33
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111

Chart 26.—North component surface wind stress for February.

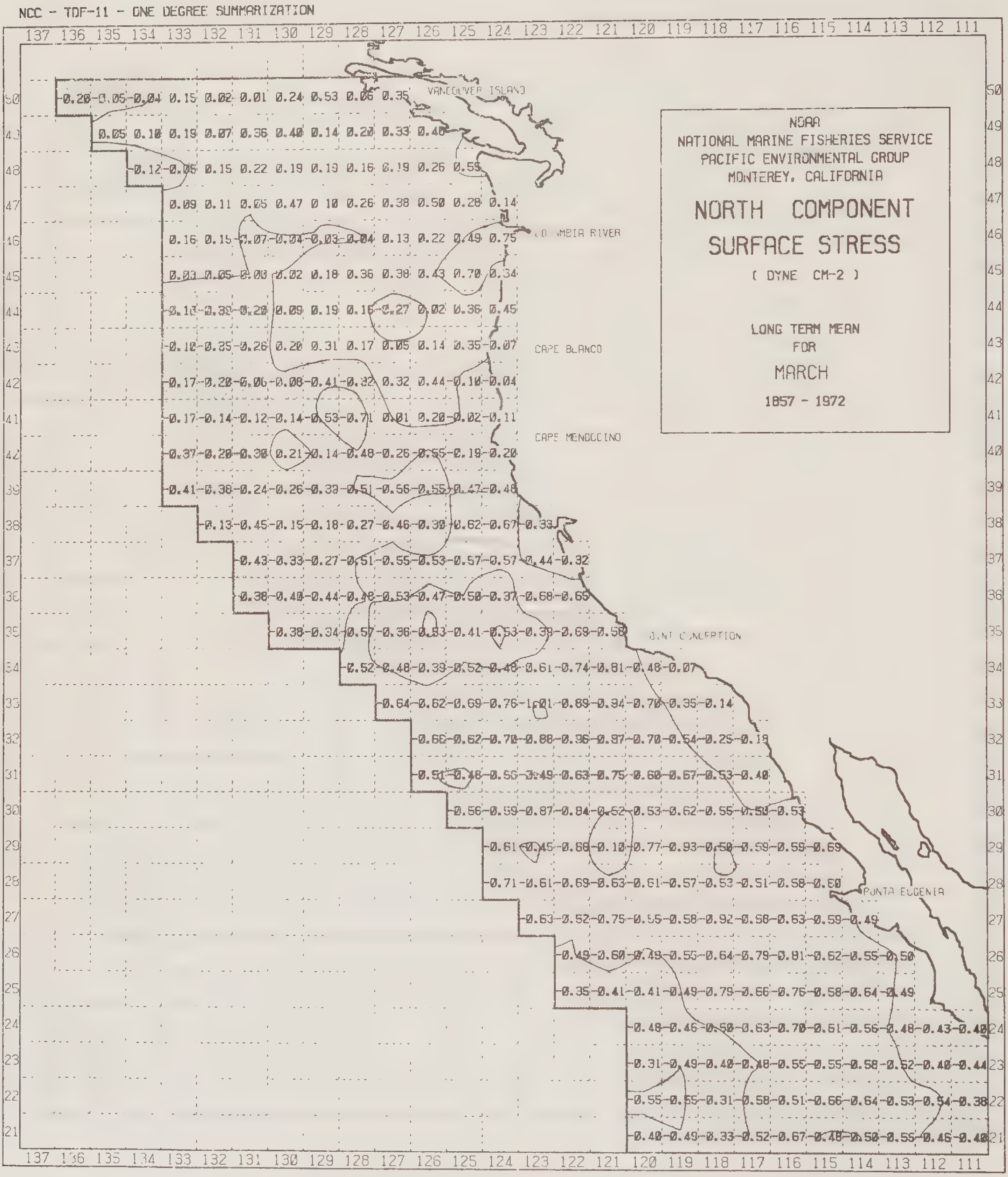

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
NORTH COMPONENT
SURFACE STRESS
(DYNE CM-2)
LONG TERM MEAN
FOR
MARCH
1857 - 1972
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
50 -0.20 -0.05 -0.04 0.15 0.02 0.01 0.24 0.53 0.06 0.35
49 0.05 0.10 0.19 0.07 0.36 0.40 0.14 0.20 0.33 0.40
48 -0.12 -0.05 0.15 0.22 0.19 0.19 0.16 0.19 0.26 0.55
47 0.09 0.11 0.05 0.47 0.10 0.26 0.38 0.50 0.28 0.14
46 0.16 0.15 -0.07 -0.04 -0.03 -0.04 0.13 0.22 0.49 0.75
45 0.03 0.05 0.00 0.02 0.18 0.36 0.38 0.43 0.70 0.34
44 -0.13 -0.39 -0.20 0.09 0.19 0.16 -0.27 0.02 0.36 0.45
43 -0.10 -0.25 -0.26 0.20 0.31 0.17 0.05 0.14 0.35 -0.07
42 -0.17 -0.20 -0.06 -0.08 -0.41 -0.32 0.32 0.44 -0.10 -0.04
41 -0.17 -0.14 -0.12 -0.14 -0.53 -0.71 0.01 0.20 -0.02 -0.11
40 -0.37 -0.20 -0.30 0.21 -0.14 -0.48 -0.26 -0.55 -0.19 -0.20
39 -0.41 -0.38 -0.24 -0.26 -0.33 -0.51 -0.56 -0.55 -0.47 -0.48
38 -0.13 -0.45 -0.15 -0.18 -0.27 -0.46 -0.30 -0.62 -0.67 -0.33
37 -0.43 -0.33 -0.27 -0.51 -0.55 -0.53 -0.57 -0.57 -0.44 -0.32
36 -0.38 -0.40 -0.44 -0.48 -0.53 -0.47 -0.50 -0.37 -0.68 -0.65
35 -0.38 -0.34 -0.57 -0.36 -0.53 -0.41 -0.53 -0.39 -0.69 -0.58
34 -0.52 -0.48 -0.39 -0.52 -0.48 -0.61 -0.74 -0.81 -0.48 -0.07
33 -0.64 -0.62 -0.69 -0.76 -1.01 -0.89 -0.94 -0.70 -0.35 -0.14
32 -0.66 -0.62 -0.70 -0.88 -0.96 -0.97 -0.70 -0.54 -0.25 -0.18
31 -0.51 -0.48 -0.56 -0.49 -0.63 -0.75 -0.60 -0.67 -0.53 -0.40
30 -0.56 -0.59 -0.87 -0.84 -0.52 -0.53 -0.62 -0.55 -0.50 -0.53
29 -0.61 -0.45 -0.66 -0.10 -0.77 -0.93 -0.50 -0.59 -0.59 -0.69
28 -0.71 -0.61 -0.69 -0.63 -0.61 -0.57 -0.53 -0.51 -0.58 -0.60
27 -0.63 -0.52 -0.75 -0.55 -0.58 -0.92 -0.58 -0.63 -0.59 -0.49
26 -0.49 -0.60 -0.49 -0.55 -0.64 -0.79 -0.81 -0.62 -0.55 -0.50
25 -0.35 -0.41 -0.41 -0.49 -0.79 -0.66 -0.76 -0.58 -0.64 -0.49
24 -0.48 -0.46 -0.50 -0.63 -0.70 -0.61 -0.56 -0.48 -0.43 -0.40
23 -0.31 -0.49 -0.40 -0.48 -0.55 -0.55 -0.58 -0.52 -0.40 -0.44
22 -0.55 -0.55 -0.31 -0.58 -0.51 -0.66 -0.64 -0.53 -0.54 -0.38
21 -0.40 -0.49 -0.33 -0.52 -0.67 -0.48 -0.50 -0.55 -0.46 -0.40

Chart 27.—North component surface wind stress for March.

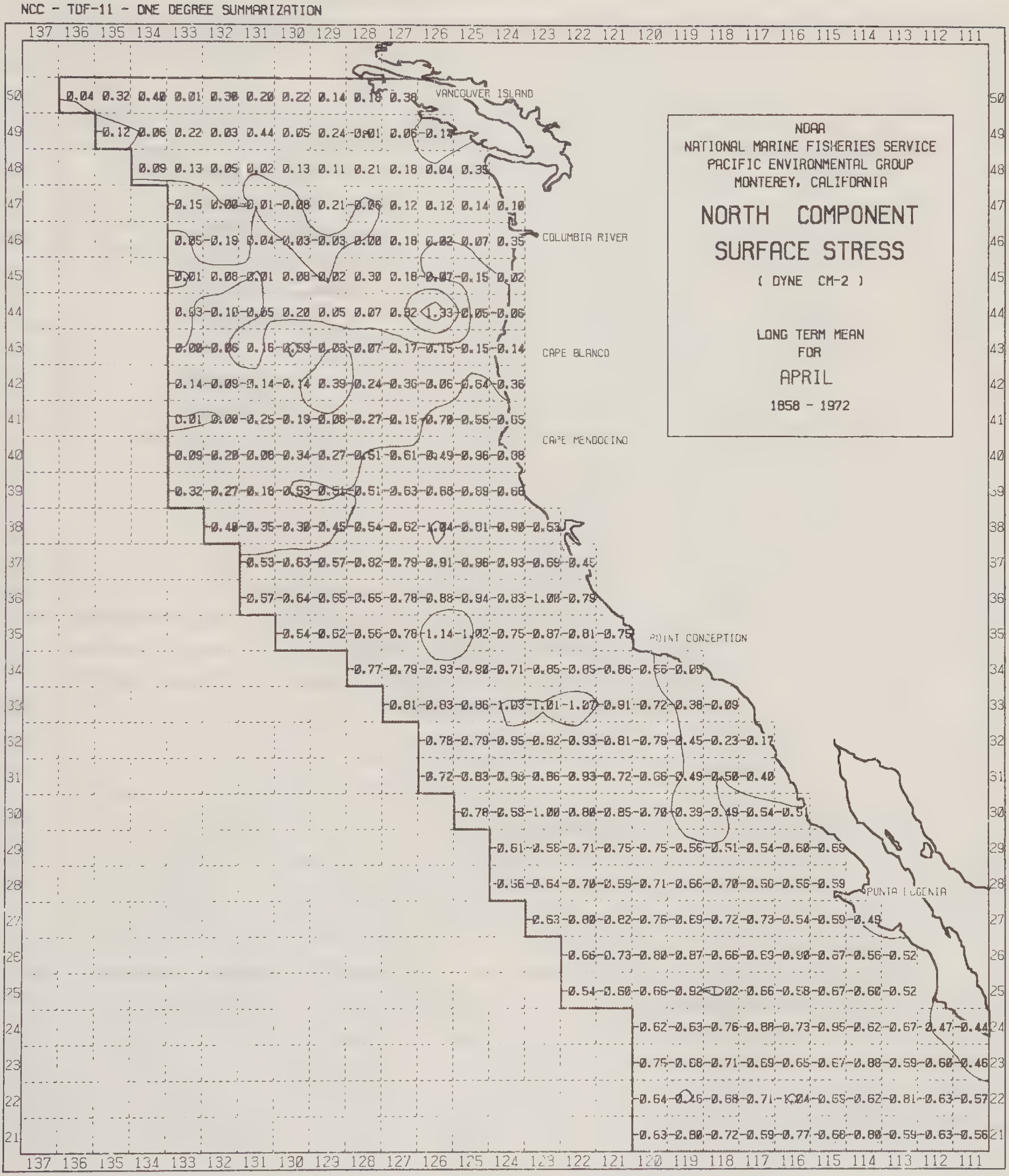

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
NORTH COMPONENT
SURFACE STRESS
(DYNE CM-2)
LONG TERM MEAN
FOR
APRIL
1858 - 1972
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21

Chart 28.—North component surface wind stress for April.

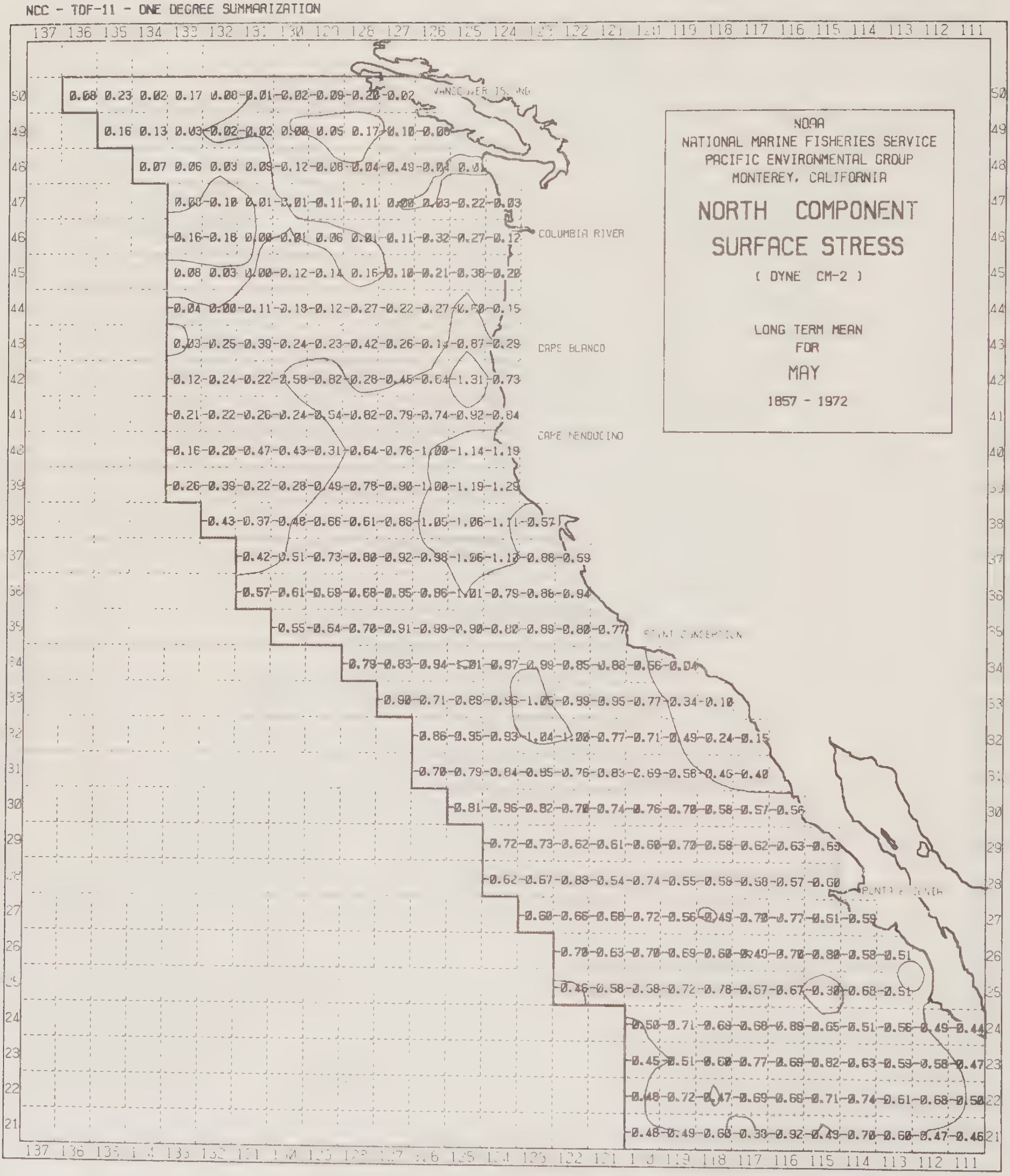

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
NORTH COMPONENT
SURFACE STRESS
(DYNE CM-2)
LONG TERM MEAN
FOR
MAY
1857 - 1972
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
0.08 0.23 0.02 0.17 0.08 -0.01 -0.02 -0.09 -0.20 -0.02
0.16 0.13 0.03 -0.02 -0.02 0.00 0.05 0.17 -0.10 -0.06
0.07 0.06 0.03 0.09 -0.12 -0.08 -0.04 -0.49 -0.04 0.01
0.00 -0.10 0.01 -0.01 -0.11 -0.11 0.00 0.03 -0.22 -0.03
-0.16 -0.18 0.00 -0.01 0.06 0.01 -0.11 -0.32 -0.27 -0.12
0.08 0.03 0.00 -0.12 -0.14 0.16 -0.10 -0.21 -0.38 -0.20
-0.04 0.00 -0.11 -0.18 -0.12 -0.27 -0.22 -0.27 -0.60 -0.15
0.03 -0.25 -0.39 -0.24 -0.23 -0.42 -0.26 -0.14 -0.87 -0.29
-0.12 -0.24 -0.22 -0.58 -0.82 -0.28 -0.45 -0.64 -1.31 -0.73
-0.21 -0.22 -0.26 -0.24 -0.54 -0.82 -0.79 -0.74 -0.92 -0.84
-0.16 -0.20 -0.47 -0.43 -0.31 -0.64 -0.76 -1.00 -1.14 -1.19
-0.26 -0.39 -0.22 -0.28 -0.49 -0.78 -0.90 -1.00 -1.19 -1.29
-0.43 -0.37 -0.48 -0.66 -0.61 -0.86 -1.05 -1.06 -1.11 -0.57
-0.42 -0.51 -0.73 -0.80 -0.92 -0.98 -1.06 -1.10 -0.88 -0.59
-0.57 -0.61 -0.69 -0.68 -0.85 -0.86 -1.01 -0.79 -0.86 -0.94
-0.55 -0.64 -0.70 -0.91 -0.99 -0.90 -0.80 -0.89 -0.80 -0.77
-0.79 -0.83 -0.94 -1.01 -0.97 -0.99 -0.85 -0.88 -0.56 -0.04
-0.90 -0.71 -0.89 -0.96 -1.05 -0.99 -0.95 -0.77 -0.34 -0.10
-0.86 -0.95 -0.93 -1.04 -1.00 -0.77 -0.71 -0.49 -0.24 -0.15
-0.70 -0.79 -0.84 -0.85 -0.76 -0.83 -0.69 -0.58 -0.46 -0.40
-0.81 -0.96 -0.82 -0.70 -0.74 -0.76 -0.70 -0.58 -0.57 -0.56
-0.72 -0.73 -0.62 -0.61 -0.60 -0.70 -0.58 -0.62 -0.63 -0.63
-0.62 -0.67 -0.83 -0.54 -0.74 -0.55 -0.58 -0.58 -0.57 -0.60
-0.60 -0.66 -0.68 -0.72 -0.56 -0.49 -0.70 -0.77 -0.61 -0.59
-0.70 -0.63 -0.70 -0.69 -0.60 -0.40 -0.70 -0.80 -0.58 -0.51
-0.46 -0.58 -0.58 -0.72 -0.78 -0.57 -0.67 -0.30 -0.68 -0.51
-0.50 -0.71 -0.68 -0.68 -0.89 -0.65 -0.51 -0.56 -0.49 -0.44
-0.45 -0.51 -0.60 -0.77 -0.69 -0.82 -0.63 -0.59 -0.58 -0.47
-0.48 -0.72 -0.47 -0.69 -0.69 -0.71 -0.74 -0.61 -0.68 -0.50
-0.48 -0.49 -0.60 -0.33 -0.92 -0.43 -0.70 -0.60 -0.47 -0.46

Chart 29.—North component surface wind stress for May.

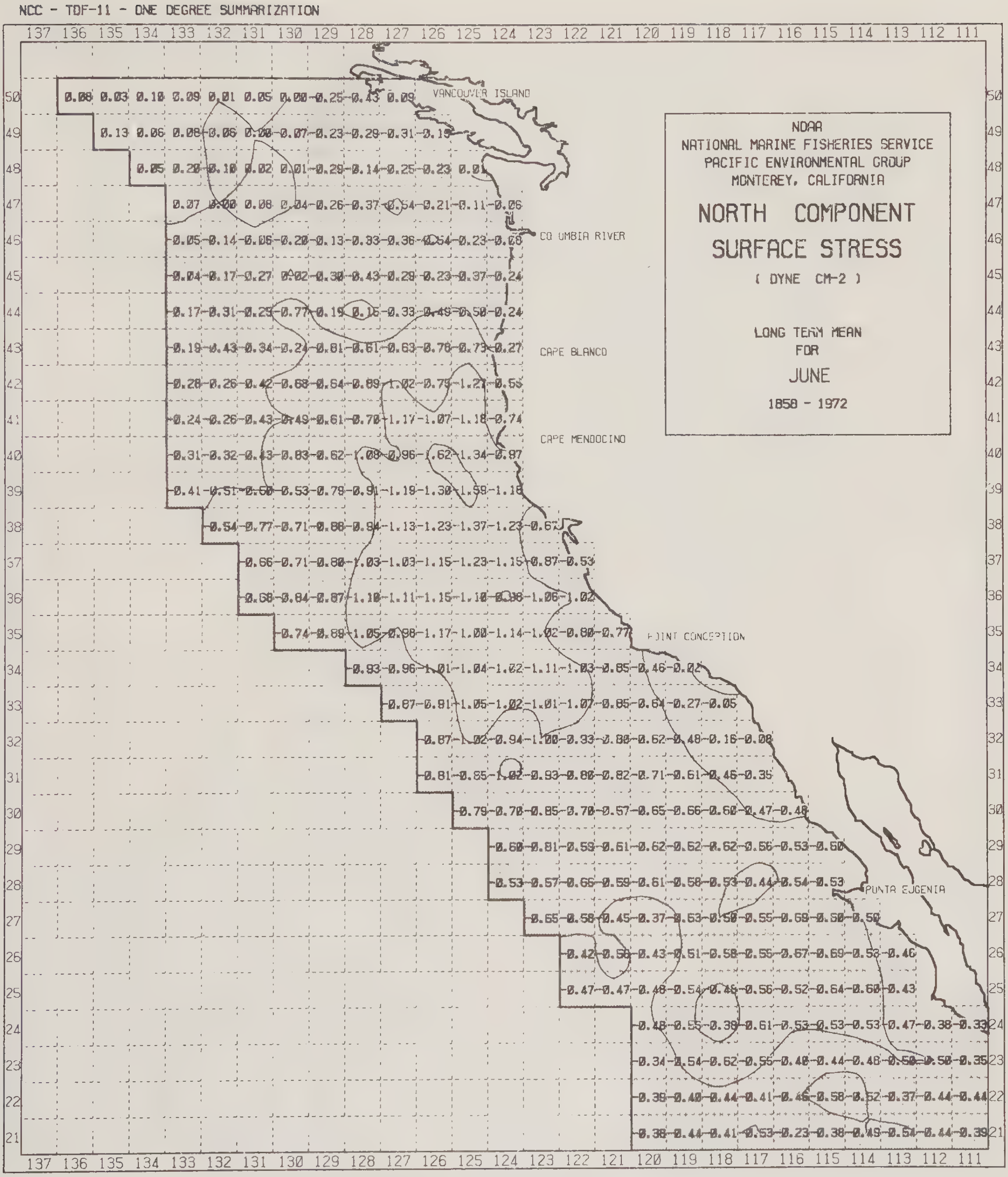

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
NORTH COMPONENT
SURFACE STRESS
(DYNE CM-2)
LONG TERM MEAN
FOR
JUNE
1850 - 1972
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
50: 0.08 0.03 0.10 0.09 0.01 0.05 0.00 -0.25 -0.43 0.09
49: 0.13 0.06 0.08 -0.06 0.00 -0.07 -0.23 -0.29 -0.31 -0.19
48: 0.05 0.20 -0.10 0.02 0.01 -0.29 -0.14 -0.25 -0.23 0.01
47: 0.27 0.00 0.06 0.04 -0.26 -0.37 -0.54 -0.21 -0.11 -0.06
46: -0.05 -0.14 -0.06 -0.20 -0.13 -0.33 -0.36 -0.54 -0.23 -0.08
45: -0.04 -0.17 -0.27 0.02 -0.30 -0.43 -0.29 -0.23 -0.37 -0.24
44: -0.17 -0.31 -0.25 -0.77 -0.19 -0.16 -0.33 -0.49 -0.50 -0.24
43: -0.19 -0.43 -0.34 -0.24 -0.81 -0.61 -0.63 -0.76 -0.79 -0.27
42: -0.28 -0.26 -0.42 -0.68 -0.64 -0.89 -1.02 -0.79 -1.27 -0.55
41: -0.24 -0.26 -0.43 -0.49 -0.61 -0.70 -1.17 -1.07 -1.18 -0.74
40: -0.31 -0.32 -0.43 -0.83 -0.62 -1.09 -0.96 -1.62 -1.34 -0.97
39: -0.41 -0.51 -0.60 -0.53 -0.79 -0.91 -1.19 -1.30 -1.59 -1.16
38: -0.54 -0.77 -0.71 -0.86 -0.84 -1.13 -1.23 -1.37 -1.23 -0.67
37: -0.66 -0.71 -0.80 -1.03 -1.03 -1.15 -1.23 -1.15 -0.87 -0.53
36: -0.68 -0.84 -0.87 -1.10 -1.11 -1.15 -1.10 -0.98 -1.06 -1.02
35: -0.74 -0.88 -1.05 -0.98 -1.17 -1.00 -1.14 -1.02 -0.80 -0.77
34: -0.93 -0.96 -1.01 -1.04 -1.02 -1.11 -1.03 -0.85 -0.46 -0.02
33: -0.87 -0.91 -1.05 -1.02 -1.01 -1.07 -0.85 -0.64 -0.27 -0.05
32: -0.87 -1.02 -0.94 -1.00 -0.33 -0.80 -0.62 -0.48 -0.16 -0.08
31: -0.81 -0.85 -1.02 -0.93 -0.80 -0.82 -0.71 -0.61 -0.46 -0.35
30: -0.79 -0.70 -0.85 -0.70 -0.57 -0.65 -0.66 -0.60 -0.47 -0.48
29: -0.60 -0.81 -0.59 -0.61 -0.62 -0.62 -0.62 -0.56 -0.53 -0.60
28: -0.53 -0.57 -0.66 -0.59 -0.61 -0.58 -0.53 -0.44 -0.54 -0.53
27: -0.65 -0.58 -0.45 -0.37 -0.63 -0.50 -0.55 -0.69 -0.50 -0.50
26: -0.42 -0.56 -0.43 -0.51 -0.58 -0.55 -0.67 -0.69 -0.53 -0.46
25: -0.47 -0.47 -0.46 -0.54 -0.48 -0.56 -0.52 -0.64 -0.60 -0.43
24: -0.48 -0.55 -0.39 -0.61 -0.53 -0.53 -0.53 -0.47 -0.38 -0.33
23: -0.34 -0.54 -0.62 -0.55 -0.40 -0.44 -0.48 -0.50 -0.50 -0.35
22: -0.39 -0.40 -0.44 -0.41 -0.46 -0.58 -0.52 -0.37 -0.44 -0.44
21: -0.38 -0.44 -0.41 -0.53 -0.23 -0.38 -0.49 -0.54 -0.44 -0.39

Chart 30.—North component surface wind stress for June.

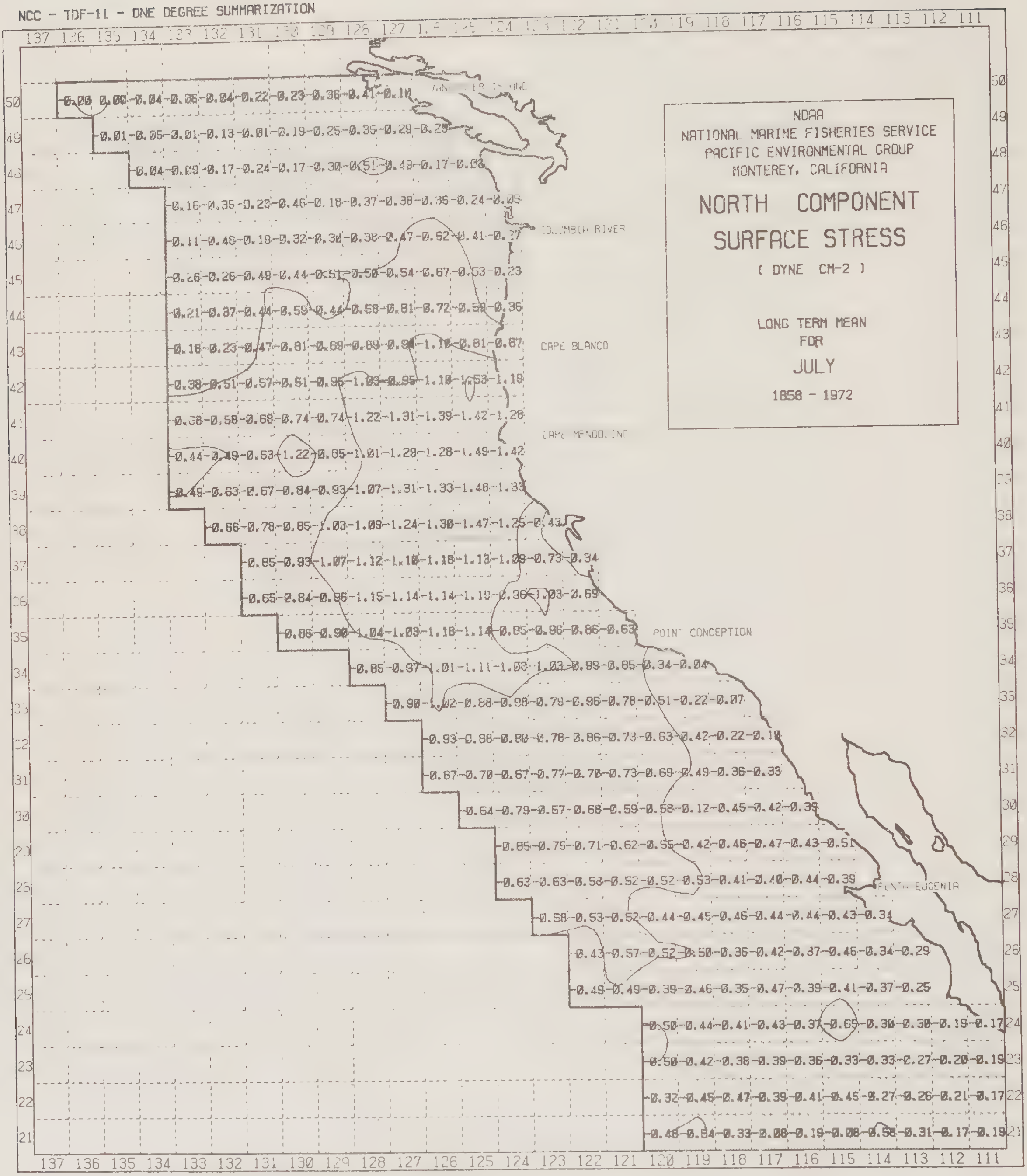
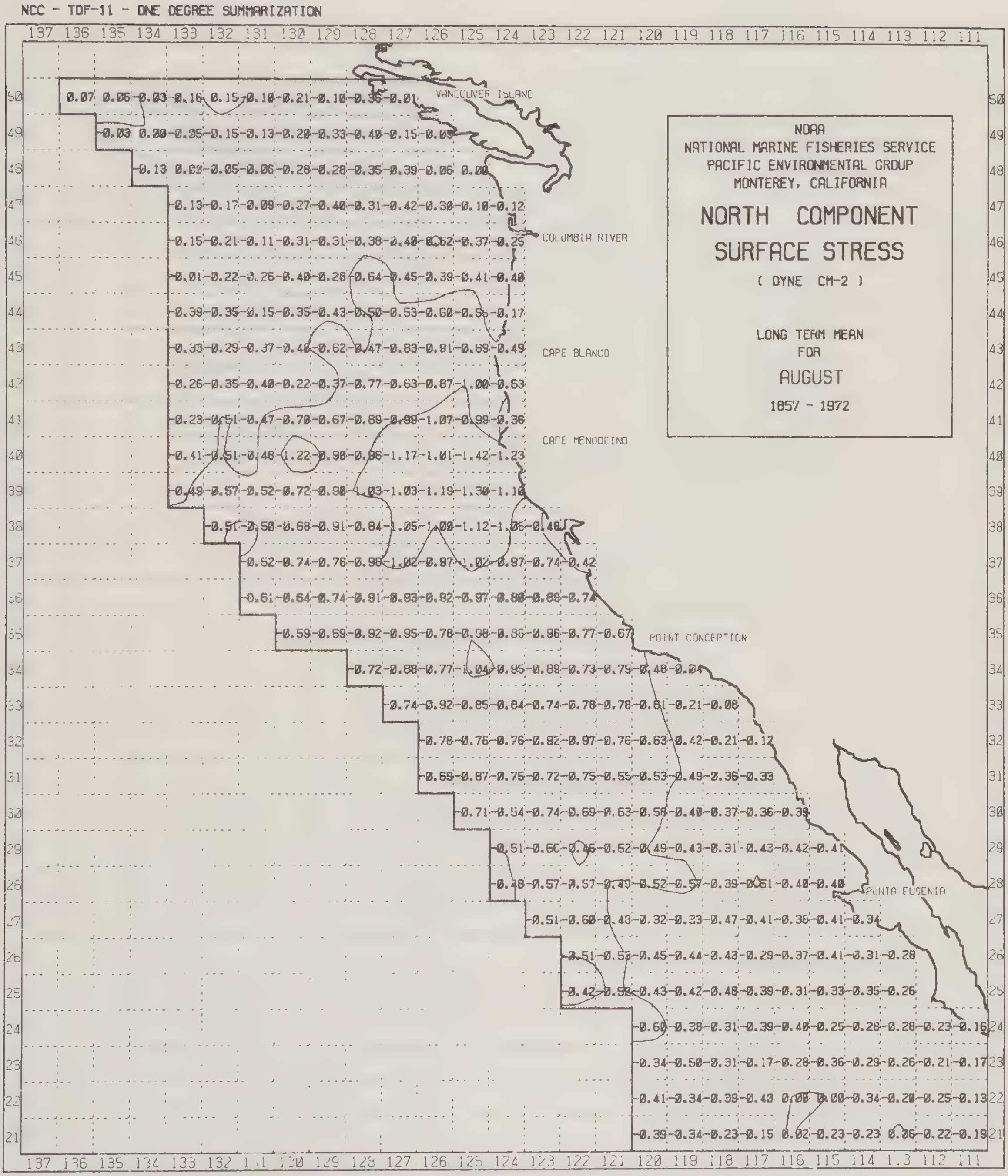

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
NORTH COMPONENT
SURFACE STRESS
(DYNE CM-2)
LONG TERM MEAN
FOR
JULY
1858 - 1972
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
-0.00 0.00 -0.04 -0.26 -0.04 -0.22 -0.23 -0.36 -0.41 -0.10
-0.01 -0.05 -0.01 -0.13 -0.01 -0.19 -0.25 -0.35 -0.29 -0.29
-0.04 -0.09 -0.17 -0.24 -0.17 -0.30 -0.51 -0.48 -0.17 -0.08
-0.16 -0.35 -0.23 -0.46 -0.18 -0.37 -0.38 -0.36 -0.24 -0.05
-0.11 -0.46 -0.18 -0.32 -0.30 -0.38 -0.47 -0.62 -0.41 -0.27
-0.26 -0.26 -0.49 -0.44 -0.51 -0.50 -0.54 -0.67 -0.53 -0.23
-0.21 -0.37 -0.44 -0.59 -0.44 -0.58 -0.81 -0.72 -0.59 -0.36
-0.18 -0.23 -0.47 -0.81 -0.69 -0.89 -0.90 -1.10 -0.81 -0.67
-0.38 -0.51 -0.57 -0.51 -0.95 -1.09 -0.95 -1.10 -1.53 -1.19
-0.38 -0.58 -0.68 -0.74 -0.74 -1.22 -1.31 -1.39 -1.42 -1.28
-0.44 -0.49 -0.63 -1.22 -0.85 -1.01 -1.29 -1.28 -1.49 -1.42
-0.49 -0.63 -0.67 -0.84 -0.93 -1.07 -1.31 -1.33 -1.48 -1.33
-0.86 -0.78 -0.85 -1.03 -1.09 -1.24 -1.30 -1.47 -1.25 -0.43
-0.85 -0.93 -1.07 -1.12 -1.10 -1.18 -1.13 -1.09 -0.73 -0.34
-0.65 -0.84 -0.96 -1.15 -1.14 -1.14 -1.19 -0.36 -1.03 -0.69
-0.86 -0.90 -1.04 -1.03 -1.18 -1.14 -0.85 -0.86 -0.86 -0.63
-0.85 -0.97 -1.01 -1.11 -1.00 -1.03 -0.99 -0.85 -0.34 -0.04
-0.90 -1.02 -0.88 -0.98 -0.79 -0.96 -0.78 -0.51 -0.22 -0.07
-0.93 -0.88 -0.80 -0.78 -0.86 -0.73 -0.63 -0.42 -0.22 -0.10
-0.87 -0.70 -0.67 -0.77 -0.70 -0.73 -0.69 -0.49 -0.36 -0.33
-0.64 -0.79 -0.57 -0.68 -0.59 -0.58 -0.12 -0.45 -0.42 -0.39
-0.85 -0.75 -0.71 -0.62 -0.55 -0.42 -0.46 -0.47 -0.43 -0.51
-0.63 -0.63 -0.53 -0.52 -0.52 -0.53 -0.41 -0.40 -0.44 -0.39
-0.58 -0.53 -0.52 -0.44 -0.45 -0.46 -0.44 -0.44 -0.43 -0.34
-0.43 -0.57 -0.52 -0.50 -0.36 -0.42 -0.37 -0.46 -0.34 -0.29
-0.49 -0.49 -0.39 -0.46 -0.35 -0.47 -0.39 -0.41 -0.37 -0.25
-0.50 -0.44 -0.41 -0.43 -0.37 -0.65 -0.30 -0.30 -0.19 -0.17
-0.50 -0.42 -0.38 -0.39 -0.36 -0.33 -0.33 -0.27 -0.20 -0.19
-0.32 -0.45 -0.47 -0.39 -0.41 -0.45 -0.27 -0.26 -0.21 -0.17
-0.48 -0.54 -0.33 -0.08 -0.19 -0.08 -0.58 -0.31 -0.17 -0.19

Chart 31.—North component surface wind stress for July.



NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
NORTH COMPONENT
SURFACE STRESS
(DYNE CM-2)
LONG TERM MEAN
FOR
AUGUST
1857 - 1972
0.07 0.06 -0.03 -0.16 0.15 -0.10 -0.21 -0.10 -0.36 -0.01
-0.03 0.00 -0.35 -0.15 -0.13 -0.20 -0.33 -0.40 -0.15 -0.05
-0.13 0.02 -0.05 -0.06 -0.28 -0.28 -0.35 -0.39 -0.06 0.00
-0.13 -0.17 -0.09 -0.27 -0.40 -0.31 -0.42 -0.30 -0.10 -0.12
-0.15 -0.21 -0.11 -0.31 -0.31 -0.38 -0.40 -0.52 -0.37 -0.25
-0.01 -0.22 -0.26 -0.40 -0.26 -0.64 -0.45 -0.39 -0.41 -0.40
-0.38 -0.35 -0.15 -0.35 -0.43 -0.50 -0.53 -0.60 -0.65 -0.17
-0.33 -0.29 -0.37 -0.40 -0.62 -0.47 -0.83 -0.81 -0.69 -0.49
-0.26 -0.35 -0.40 -0.22 -0.37 -0.77 -0.63 -0.87 -1.00 -0.63
-0.23 -0.51 -0.47 -0.70 -0.67 -0.89 -0.99 -1.07 -0.99 -0.36
-0.41 -0.51 -0.48 -1.22 -0.90 -0.86 -1.17 -1.01 -1.42 -1.23
-0.49 -0.57 -0.52 -0.72 -0.90 -1.03 -1.03 -1.19 -1.30 -1.10
-0.51 -0.50 -0.68 -0.91 -0.84 -1.05 -1.00 -1.12 -1.06 -0.48
-0.52 -0.74 -0.76 -0.98 -1.02 -0.97 -1.02 -0.87 -0.74 -0.42
-0.61 -0.64 -0.74 -0.91 -0.93 -0.92 -0.87 -0.80 -0.88 -0.74
-0.59 -0.69 -0.92 -0.95 -0.78 -0.98 -0.86 -0.96 -0.77 -0.67
-0.72 -0.88 -0.77 -1.04 -0.95 -0.89 -0.73 -0.79 -0.48 -0.04
-0.74 -0.92 -0.85 -0.84 -0.74 -0.78 -0.78 -0.61 -0.21 -0.08
-0.78 -0.76 -0.76 -0.92 -0.97 -0.76 -0.63 -0.42 -0.21 -0.12
-0.69 -0.87 -0.75 -0.72 -0.75 -0.55 -0.53 -0.49 -0.36 -0.33
-0.71 -0.54 -0.74 -0.69 -0.63 -0.58 -0.40 -0.37 -0.36 -0.39
-0.51 -0.60 -0.46 -0.62 -0.49 -0.43 -0.31 -0.43 -0.42 -0.41
-0.48 -0.57 -0.57 -0.49 -0.52 -0.57 -0.39 -0.51 -0.40 -0.40
-0.51 -0.60 -0.43 -0.32 -0.23 -0.47 -0.41 -0.36 -0.41 -0.34
-0.51 -0.53 -0.45 -0.44 -0.43 -0.29 -0.37 -0.41 -0.31 -0.28
-0.42 -0.58 -0.43 -0.42 -0.48 -0.39 -0.31 -0.33 -0.35 -0.26
-0.60 -0.38 -0.31 -0.39 -0.40 -0.25 -0.28 -0.28 -0.23 -0.16
-0.34 -0.50 -0.31 -0.17 -0.28 -0.36 -0.29 -0.26 -0.21 -0.17
-0.41 -0.34 -0.39 -0.43 0.08 0.00 -0.34 -0.20 -0.25 -0.13
-0.39 -0.34 -0.23 -0.15 0.02 -0.23 -0.23 0.06 -0.22 -0.19

Chart 32.—North component surface wind stress for August.

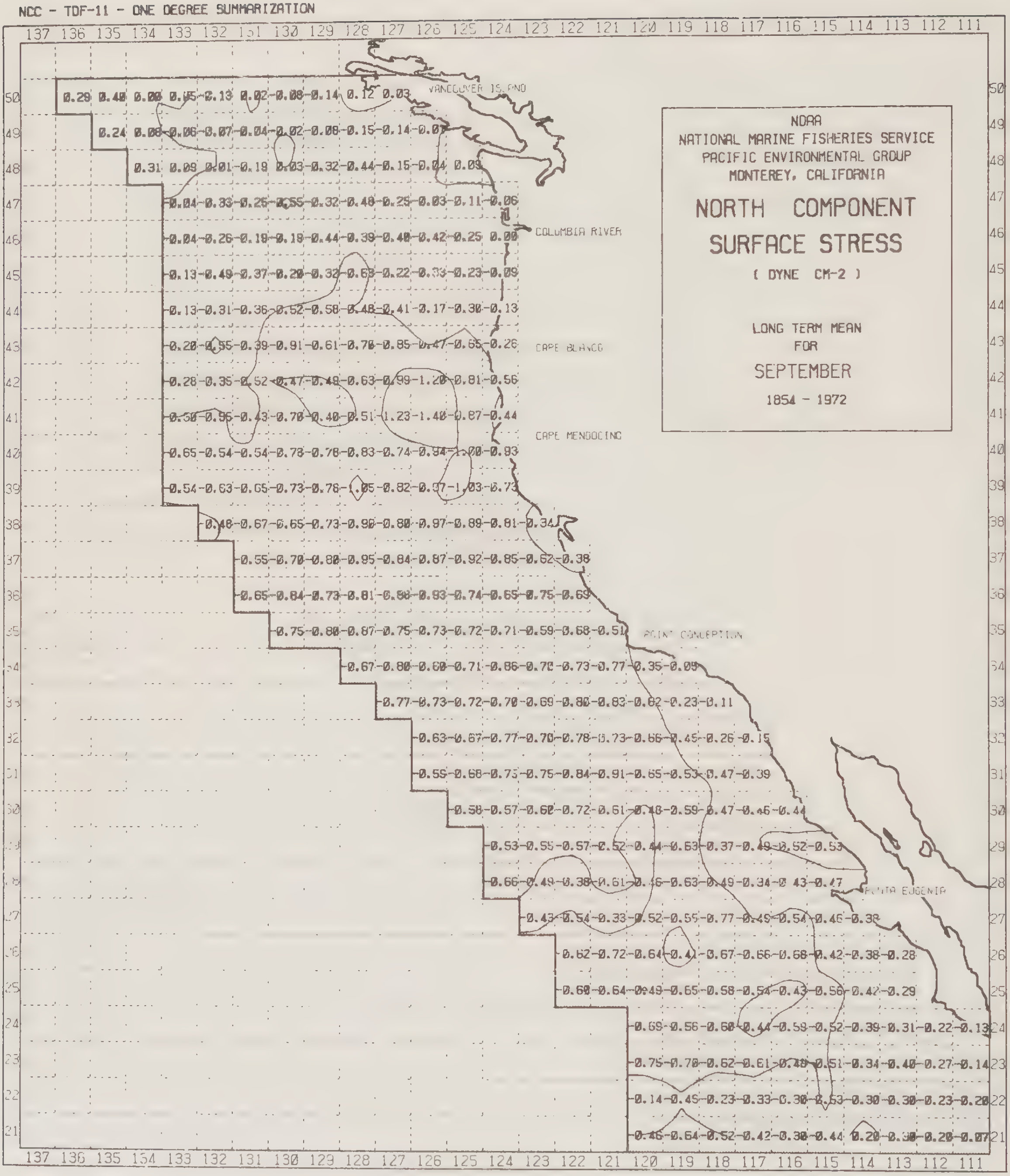

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
NORTH COMPONENT
SURFACE STRESS
(DYNE CM-2)
LONG TERM MEAN
FOR
SEPTEMBER
1854 - 1972
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA

Chart 33.—North component surface wind stress for September.

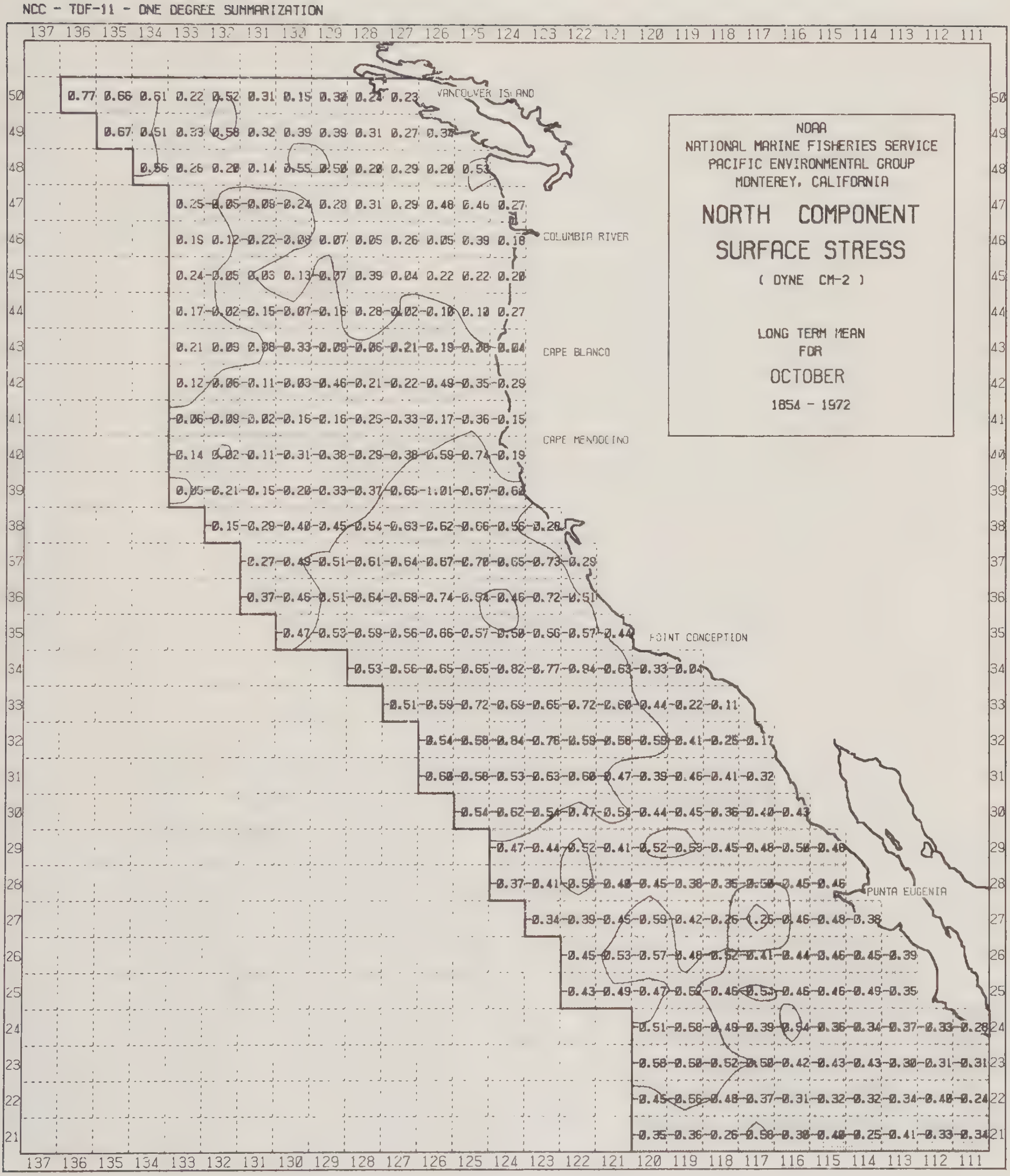
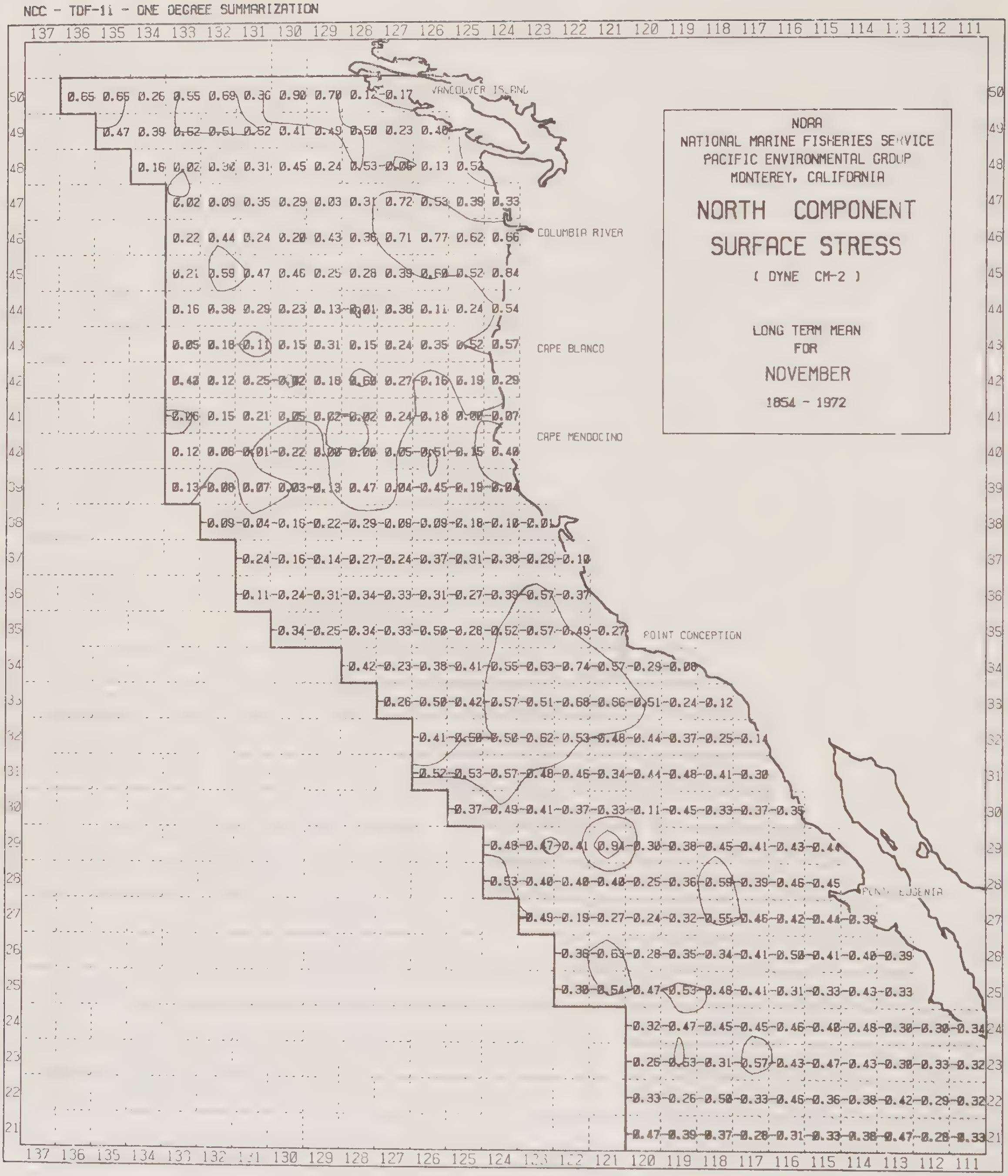

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
NORTH COMPONENT
SURFACE STRESS
(DYNE CM-2)
LONG TERM MEAN
FOR
OCTOBER
1854 - 1972
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
50 0.77 0.66 0.61 0.22 0.52 0.31 0.15 0.30 0.24 0.23
49 0.67 0.51 0.33 0.58 0.32 0.39 0.39 0.31 0.27 0.37
48 0.56 0.26 0.20 0.14 0.55 0.50 0.20 0.29 0.20 0.53
47 0.25-0.05-0.08-0.24 0.28 0.31 0.29 0.48 0.46 0.27
46 0.15 0.12-0.22-0.08 0.07 0.05 0.26 0.05 0.39 0.18
45 0.24-0.05 0.03 0.13-0.07 0.39 0.04 0.22 0.22 0.20
44 0.17-0.02-0.15-0.07-0.16 0.28-0.02-0.10 0.10 0.27
43 0.21 0.09 0.08-0.33-0.09-0.06-0.21-0.19-0.20-0.04
42 0.12-0.06-0.11-0.03-0.46-0.21-0.22-0.49-0.35-0.29
41 -0.06-0.09-0.02-0.16-0.16-0.25-0.33-0.17-0.36-0.15
40 -0.14 0.02-0.11-0.31-0.38-0.29-0.38-0.59-0.74-0.19
39 0.05-0.21-0.15-0.20-0.33-0.37-0.65-1.01-0.67-0.62
38 -0.15-0.29-0.40-0.45-0.54-0.63-0.62-0.66-0.56-0.28
37 -0.27-0.49-0.51-0.61-0.64-0.67-0.70-0.65-0.73-0.29
36 -0.37-0.46-0.51-0.64-0.69-0.74-0.54-0.46-0.72-0.51
35 -0.47-0.53-0.59-0.56-0.66-0.57-0.50-0.56-0.57-0.44
34 -0.53-0.56-0.65-0.65-0.82-0.77-0.84-0.63-0.33-0.04
33 -0.51-0.59-0.72-0.69-0.65-0.72-0.60-0.44-0.22-0.11
32 -0.54-0.58-0.84-0.76-0.59-0.58-0.59-0.41-0.25-0.17
31 -0.60-0.58-0.53-0.63-0.60-0.47-0.39-0.46-0.41-0.32
30 -0.54-0.62-0.54-0.47-0.54-0.44-0.45-0.36-0.40-0.43
29 -0.47-0.44-0.52-0.41-0.52-0.53-0.45-0.48-0.50-0.48
28 -0.37-0.41-0.58-0.40-0.45-0.38-0.35-0.50-0.45-0.46
27 -0.34-0.39-0.45-0.59-0.42-0.26-0.26-0.46-0.48-0.38
26 -0.45-0.53-0.57-0.48-0.52-0.41-0.44-0.46-0.45-0.39
25 -0.43-0.49-0.47-0.52-0.46-0.53-0.46-0.46-0.49-0.35
24 -0.51-0.58-0.49-0.39-0.54-0.36-0.34-0.37-0.33-0.28
23 -0.58-0.50-0.52-0.50-0.42-0.43-0.43-0.30-0.31-0.31
22 -0.45-0.56-0.48-0.37-0.31-0.32-0.32-0.34-0.40-0.24
21 -0.35-0.36-0.26-0.50-0.38-0.40-0.25-0.41-0.33-0.34
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111

Chart 34.—North component surface wind stress for October.



NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
NORTH COMPONENT
SURFACE STRESS
(DYNE CM-2)
LONG TERM MEAN
FOR
NOVEMBER
1854 - 1972
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
0.65 0.65 0.26 0.55 0.69 0.36 0.90 0.70 0.12 -0.17
0.47 0.39 0.62 0.51 0.52 0.41 0.49 0.50 0.23 0.48
0.16 0.02 0.30 0.31 0.45 0.24 0.53 -0.06 0.13 0.52
0.02 0.09 0.35 0.29 0.03 0.31 0.72 0.53 0.39 0.33
0.22 0.44 0.24 0.20 0.43 0.36 0.71 0.77 0.62 0.66
0.21 0.59 0.47 0.46 0.25 0.28 0.39 0.60 0.52 0.84
0.16 0.38 0.29 0.23 0.13 -0.01 0.38 0.11 0.24 0.54
0.05 0.18 0.11 0.15 0.31 0.15 0.24 0.35 0.52 0.57
0.43 0.12 0.25 -0.02 0.18 0.60 0.27 -0.16 0.19 0.29
-0.06 0.15 0.21 0.05 0.02 -0.02 0.24 -0.18 0.00 -0.07
0.12 0.08 -0.01 -0.22 0.00 0.00 0.05 -0.51 -0.15 0.40
0.13 -0.08 0.07 0.03 -0.13 0.47 0.04 -0.45 -0.19 -0.04
-0.09 -0.04 -0.16 -0.22 -0.29 -0.08 -0.09 -0.18 -0.10 -0.01
-0.24 -0.16 -0.14 -0.27 -0.24 -0.37 -0.31 -0.38 -0.29 -0.10
-0.11 -0.24 -0.31 -0.34 -0.33 -0.31 -0.27 -0.39 -0.57 -0.37
-0.34 -0.25 -0.34 -0.33 -0.50 -0.28 -0.52 -0.57 -0.49 -0.27
-0.42 -0.23 -0.38 -0.41 -0.55 -0.63 -0.74 -0.57 -0.29 -0.08
-0.26 -0.50 -0.42 -0.57 -0.51 -0.68 -0.66 -0.51 -0.24 -0.12
-0.41 -0.50 -0.50 -0.62 -0.53 -0.48 -0.44 -0.37 -0.25 -0.14
-0.52 -0.53 -0.57 -0.48 -0.46 -0.34 -0.44 -0.48 -0.41 -0.30
-0.37 -0.49 -0.41 -0.37 -0.33 -0.11 -0.45 -0.33 -0.37 -0.35
-0.48 -0.47 -0.41 -0.91 -0.30 -0.38 -0.45 -0.41 -0.43 -0.44
-0.53 -0.40 -0.40 -0.40 -0.25 -0.36 -0.59 -0.39 -0.46 -0.45
-0.49 -0.19 -0.27 -0.24 -0.32 -0.55 -0.46 -0.42 -0.44 -0.39
-0.36 -0.63 -0.28 -0.35 -0.34 -0.41 -0.50 -0.41 -0.40 -0.39
-0.30 -0.54 -0.47 -0.53 -0.48 -0.41 -0.31 -0.33 -0.43 -0.33
-0.32 -0.47 -0.45 -0.45 -0.46 -0.40 -0.48 -0.30 -0.30 -0.34
-0.26 -0.53 -0.31 -0.57 -0.43 -0.47 -0.43 -0.30 -0.33 -0.32
-0.33 -0.26 -0.50 -0.33 -0.45 -0.36 -0.38 -0.42 -0.29 -0.32
-0.47 -0.39 -0.37 -0.28 -0.31 -0.33 -0.38 -0.47 -0.28 -0.33

Chart 35.—North component surface wind stress for November.

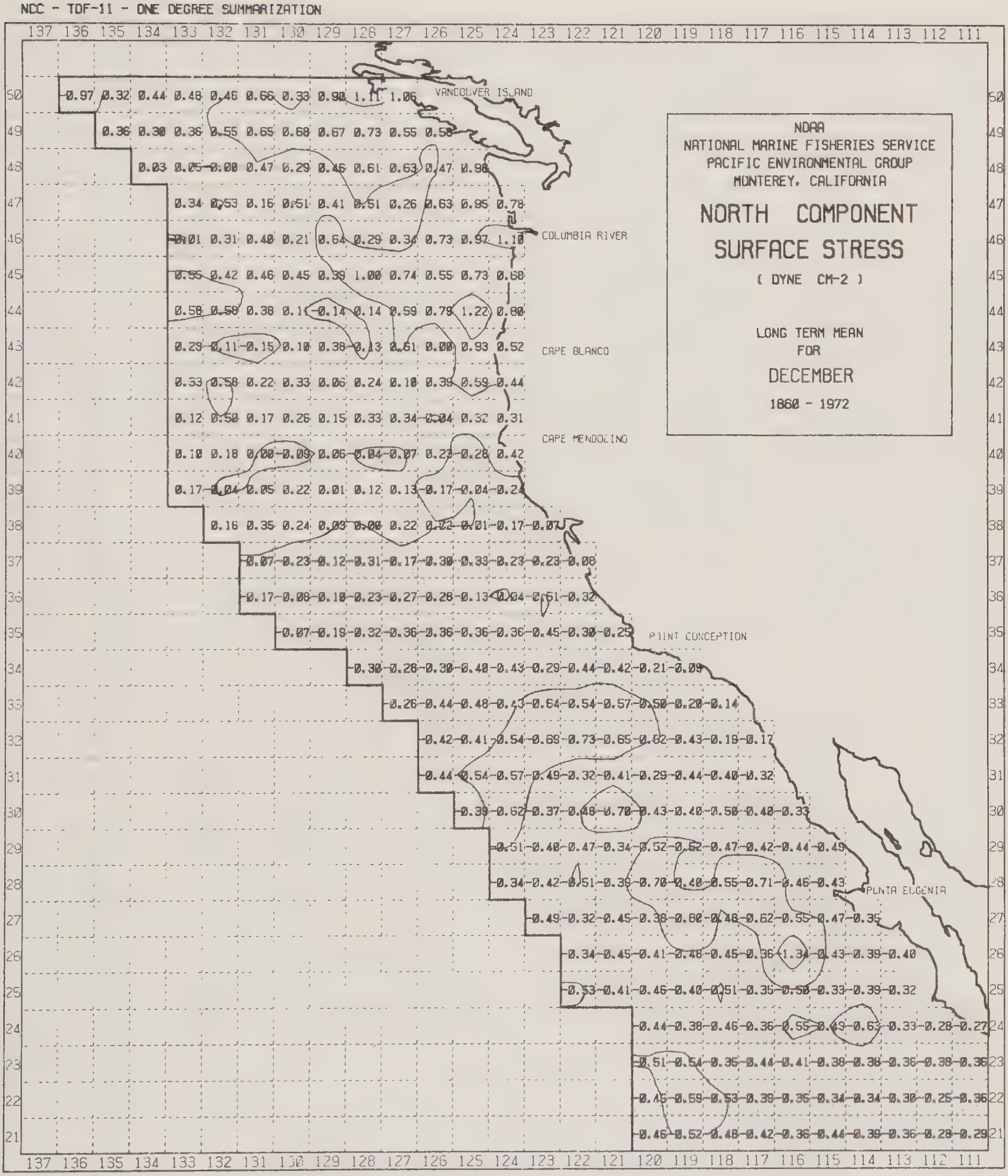

NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 -0.97 0.32 0.44 0.48 0.46 0.66 0.33 0.90 1.11 1.06
49 0.36 0.30 0.36 0.55 0.65 0.68 0.67 0.73 0.55 0.58
48 0.03 0.05-0.00 0.47 0.29 0.46 0.61 0.63 0.47 0.96
47 0.34 0.53 0.16 0.51 0.41 0.51 0.26 0.63 0.95 0.78
46 -0.01 0.31 0.40 0.21 0.64 0.29 0.34 0.73 0.97 1.10
45 -0.55 0.42 0.46 0.45 0.39 1.00 0.74 0.55 0.73 0.68
44 0.58 0.58 0.38 0.11-0.14 0.14 0.59 0.79 1.22 0.80
43 0.29 0.11-0.15 0.10 0.38-0.13 0.61 0.00 0.93 0.52
42 0.33 0.58 0.22 0.33 0.06 0.24 0.10 0.39 0.59 0.44
41 0.12 0.50 0.17 0.26 0.15 0.33 0.34-0.04 0.32 0.31
40 0.10 0.18 0.00-0.09 0.06-0.04-0.07 0.23-0.28 0.42
39 0.17-0.04 0.05 0.22 0.01 0.12 0.13-0.17-0.04-0.24
38 0.16 0.35 0.24 0.03 0.00 0.22 0.22-0.01-0.17-0.07
37 -0.07-0.23-0.12-0.31-0.17-0.30-0.33-0.23-0.23-0.08
36 -0.17-0.08-0.10-0.23-0.27-0.28-0.13-0.04-0.51-0.32
35 -0.07-0.19-0.32-0.36-0.36-0.36-0.36-0.45-0.30-0.25
34 -0.30-0.28-0.30-0.40-0.43-0.29-0.44-0.42-0.21-0.09
33 -0.26-0.44-0.48-0.43-0.64-0.54-0.57-0.50-0.20-0.14
32 -0.42-0.41-0.54-0.69-0.73-0.65-0.62-0.43-0.19-0.17
31 -0.44-0.54-0.57-0.49-0.32-0.41-0.29-0.44-0.40-0.32
30 -0.39-0.62-0.37-0.48-0.70-0.43-0.40-0.50-0.40-0.33
29 -0.51-0.40-0.47-0.34-0.52-0.62-0.47-0.42-0.44-0.49
28 -0.34-0.42-0.51-0.39-0.70-0.40-0.55-0.71-0.46-0.43
27 -0.49-0.32-0.45-0.38-0.80-0.48-0.62-0.55-0.47-0.35
26 -0.34-0.45-0.41-0.48-0.45-0.36-1.34-0.43-0.39-0.40
25 -0.53-0.41-0.46-0.40-0.51-0.35-0.50-0.33-0.39-0.32
24 -0.44-0.38-0.46-0.36-0.55-0.49-0.63-0.33-0.28-0.27
23 -0.51-0.54-0.35-0.44-0.41-0.38-0.38-0.36-0.38-0.36
22 -0.45-0.59-0.53-0.39-0.35-0.34-0.34-0.30-0.25-0.36
21 -0.46-0.52-0.48-0.42-0.36-0.44-0.39-0.36-0.28-0.29
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
NORTH COMPONENT
SURFACE STRESS
(DYNE CM-2)
LONG TERM MEAN
FOR
DECEMBER
1860 - 1972

Chart 36.—North component surface wind stress for December.

APPENDIX II

Standard Errors of the Means

The following tables list the computed standard errors of the monthly means by 1-degree square area for the eastward and northward components of the resultant surface wind stress. The standard errors of the means are defined by Equation (3). Each page contains values for 30 1-degree squares blocked in groups of 10. Within each group of 10, all 1-degree squares are defined by a common latitude. The first set of values corresponds to the 1-degree square immediately adjacent to the coast. The final tabulations refer to the 1-degree square farthest from the coast.

The standard error of the mean is tabulated for each month and square. The latitude and longitude of the center of the 1-degree square is listed at the left. The first two numbers below each month are the standard errors of the means for the eastward and northward components, respectively. The units are dyne cm^{-2}. The last value is the number of observations.

LAT/LON	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
21 N	.04	.03	.03	.03	.03	.04	.06	.04	.08	.06	.08	.02
111 W	.05	.03	.04	.05	.04	.04	.04	.04	.06	.04	.05	.03
	74	71	95	75	88	87	101	85	107	95	81	94
21 N	.03	.02	.02	.03	.04	.03	.08	.11	.08	.04	.04	.04
112 W	.05	.03	.07	.07	.06	.05	.06	.07	.08	.06	.04	.04
	51	68	52	48	61	66	57	35	57	45	46	57
21 N	.04	.11	.04	.04	.05	.04	.05	.15	.08	.04	.08	.05
113 W	.06	.08	.10	.09	.08	.07	.06	.16	.16	.10	.10	.05
	35	50	38	39	39	39	40	25	33	38	37	58
21 N	.04	.10	.04	.07	.05	.08	.08	.15	.35	.07	.03	.05
114 W	.08	.07	.08	.17	.11	.10	.24	.16	.28	.04	.07	.08
	41	39	33	22	24	21	32	18	23	28	32	42
21 N	.16	.09	.08	.08	.05	.06	.03	.05	.08	.07	.03	.04
115 W	.09	.10	.07	.13	.06	.08	.02	.08	.11	.11	.08	.06
	29	26	35	18	23	23	31	17	19	20	27	40
21 N	.15	.04	.07	.09	.10	.07	.08	.14	.20	.08	.04	.03
116 W	.12	.06	.09	.14	.14	.07	.12	.16	.15	.06	.09	.06
	26	28	32	15	13	14	26	15	18	18	18	25
21 N	.06	.03	.07	.11	.05	.05	.16	.13	.14	.09	.02	.04
117 W	.09	.06	.09	.09	.10	.09	.08	.19	.10	.09	.06	.07
	38	26	25	19	12	22	15	21	23	22	24	26
21 N	.09	.10	.06	.14	.08	.08	.12	.19	.11	.03	.05	.05
118 W	.08	.05	.07	.14	.12	.06	.09	.24	.15	.03	.08	.08
	34	21	24	18	19	19	22	18	21	38	23	34
21 N	.09	.07	.06	.11	.04	.09	.16	.11	.08	.04	.04	.07
119 W	.08	.08	.09	.11	.10	.06	.13	.06	.18	.05	.06	.07
	24	26	30	27	19	27	21	22	30	33	43	37
21 N	.09	.05	.06	.05	.06	.06	.12	.05	.07	.09	.05	.08
120 W	.10	.06	.05	.09	.07	.05	.07	.09	.07	.13	.05	.06
	24	34	30	28	38	31	39	34	37	40	40	27
22 N	.02	.03	.02	.04	.02	.03	.03	.03	.07	.03	.02	.03
111 W	.04	.03	.03	.05	.03	.03	.02	.03	.07	.03	.02	.05
	128	101	164	122	169	150	143	150	161	160	150	120
22 N	.02	.02	.03	.06	.03	.03	.02	.15	.04	.04	.02	.03
112 W	.04	.04	.05	.05	.05	.04	.03	.08	.04	.04	.03	.05
	73	60	78	80	99	117	105	116	110	100	90	69
22 N	.03	.04	.03	.05	.03	.03	.03	.04	.09	.03	.03	.06
113 W	.04	.11	.06	.12	.07	.05	.03	.05	.11	.04	.05	.04
	51	47	67	57	67	75	84	68	70	73	77	57
22 N	.03	.04	.04	.02	.05	.03	.04	.09	.11	.03	.04	.03
114 W	.06	.09	.09	.07	.08	.07	.04	.07	.10	.08	.05	.04
	34	42	45	52	53	50	61	35	58	45	38	66
22 N	.07	.10	.06	.04	.05	.03	.05	.19	.09	.07	.04	.07
115 W	.09	.10	.09	.10	.09	.09	.07	.18	.07	.07	.07	.06
	37	30	54	38	36	37	32	34	31	34	22	30
22 N	.06	.05	.04	.11	.05	.08	.03	.32	.26	.08	.04	.07
116 W	.10	.10	.12	.19	.11	.09	.07	.29	.29	.06	.07	.06
	24	30	32	15	32	30	26	17	24	21	32	33
22 N	.05	.05	.08	.05	.07	.08	.07	.13	.12	.05	.06	.05
117 W	.11	.09	.10	.11	.14	.12	.10	.27	.10	.06	.07	.05
	33	29	34	23	19	15	21	17	17	25	26	27
22 N	.06	.11	.04	.10	.08	.06	.15	.05	.21	.05	.06	.05
118 W	.09	.11	.06	.13	.11	.12	.14	.12	.17	.07	.09	.07
	28	27	33	21	17	18	15	17	17	19	23	34
22 N	.07	.07	.08	.07	.10	.04	.06	.12	.19	.10	.12	.05
119 W	.08	.27	.08	.05	.10	.06	.12	.10	.18	.07	.07	.09
	31	24	24	25	19	24	19	26	21	21	26	32
22 N	.07	.08	.07	.09	.04	.17	.08	.14	.11	.07	.06	.07
120 W	.08	.10	.06	.08	.07	.14	.10	.13	.14	.07	.06	.08
	33	26	31	23	38	17	20	19	22	23	34	20
23 N	.01	.01	.01	.01	.01	.01	.01	.02	.01	.01	.01	.03
111 W	.01	.01	.01	.01	.01	.01	0.00	.03	.01	.01	.01	.01
	1059	1030	1125	1159	1241	1128	1178	1152	1132	1199	1083	986
23 N	.02	.02	.02	.03	.03	.02	.02	.04	.03	.02	.02	.03
112 W	.02	.03	.03	.04	.03	.03	.01	.03	.03	.02	.03	.05
	155	124	146	135	192	245	203	181	206	187	154	140
23 N	.03	.03	.06	.03	.03	.05	.02	.04	.04	.03	.02	.06
113 W	.09	.04	.06	.06	.05	.05	.03	.05	.10	.04	.04	.11
	47	48	47	54	78	78	76	72	79	75	70	47
23 N	.04	.02	.04	.05	.03	.03	.02	.04	.05	.04	.03	.06
114 W	.04	.05	.08	.13	.06	.05	.03	.04	.06	.06	.05	.09
	45	44	49	59	79	71	84	96	74	73	59	47
23 N	.11	.03	.04	.03	.03	.02	.03	.05	.04	.04	.05	.05
115 W	.04	.07	.06	.06	.09	.05	.04	.05	.06	.04	.05	.07
	42	45	55	67	65	71	62	52	71	68	55	57
23 N	.04	.07	.04	.05	.03	.05	.03	.07	.05	.04	.05	.06
116 W	.07	.09	.06	.07	.07	.06	.05	.04	.08	.06	.06	.05
	42	37	48	46	63	46	62	50	51	47	45	54
23 N	.09	.04	.06	.05	.06	.04	.04	.16	.09	.06	.09	.05
117 W	.10	.11	.07	.12	.09	.07	.05	.19	.09	.08	.10	.04
	30	34	60	38	48	46	43	28	40	38	33	52
23 N	.05	.10	.03	.05	.06	.06	.05	.16	.11	.06	.06	.04
118 W	.08	.10	.08	.10	.08	.10	.06	.16	.11	.06	.06	.05
	34	29	37	33	36	27	32	22	29	32	26	38
23 N	.06	.05	.03	.06	.05	.06	.06	.07	.10	.07	.17	.10
119 W	.08	.09	.09	.09	.07	.08	.08	.12	.11	.09	.10	.08
	35	38	38	33	38	39	30	16	24	26	24	37
23 N	.10	.05	.06	.11	.04	.05	.08	.08	.07	.08	.14	.06
120 W	.10	.06	.10	.14	.06	.09	.17	.09	.10	.10	.08	.08
	37	30	21	17	22	23	17	22	24	18	32	42

LAT/LON	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
24 N 111 W	.01 .01 572	.01 .01 494	.01 .01 590	.01 .01 587	.02 .01 591	.01 .01 603	.01 .01 596	.01 .01 602	.03 .06 566	.01 .01 535	.01 .01 594	.01 .01 504
24 N 112 W	0.00 .01 1226	.01 .01 1209	.02 .01 1375	.01 .01 1380	.01 .01 1458	.01 .01 1398	.01 0.00 1453	.01 .01 1324	.01 .01 1382	0.00 .01 1379	0.00 .01 1336	.01 .01 1208
24 N 113 W	.02 .04 143	.03 .04 142	.03 .03 195	.03 .05 150	.02 .03 176	.02 .03 210	.02 .02 193	.02 .02 223	.03 .03 214	.03 .03 177	.02 .02 172	.02 .03 141
24 N 114 W	.07 .06 42	.06 .09 39	.05 .08 45	.05 .07 38	.04 .05 58	.04 .05 54	.03 .05 54	.04 .06 70	.05 .06 78	.04 .05 62	.05 .08 44	.14 .18 25
24 N 115 W	.07 .09 29	.05 .08 31	.05 .08 39	.07 .15 46	.04 .07 59	.07 .10 49	.03 .06 87	.04 .05 51	.05 .06 68	.05 .05 56	.03 .07 44	.07 .10 22
24 N 116 W	.05 .07 35	.03 .06 43	.08 .09 37	.04 .08 55	.04 .08 67	.05 .06 68	.02 .04 75	.06 .05 73	.04 .08 56	.03 .05 59	.02 .06 56	.04 .10 39
24 N 117 W	.05 .07 43	.06 .15 29	.04 .09 33	.06 .18 44	.04 .08 62	.03 .07 71	.03 .06 71	.04 .05 62	.04 .06 60	.03 .05 56	.04 .05 51	.04 .05 57
24 N 118 W	.05 .06 35	.06 .08 47	.04 .06 49	.05 .09 40	.05 .08 52	.03 .06 52	.02 .06 47	.09 .06 44	.05 .08 50	.04 .05 57	.04 .06 48	.07 .06 39
24 N 119 W	.03 .05 40	.11 .13 41	.08 .07 56	.05 .10 44	.04 .07 57	.03 .09 39	.06 .08 53	.13 .08 38	.05 .09 36	.04 .07 40	.08 .08 36	.04 .04 50
24 N 120 W	.07 .08 47	.04 .07 55	.03 .08 57	.05 .08 45	.05 .06 41	.05 .09 30	.08 .05 38	.15 .10 29	.08 .11 35	.07 .05 38	.05 .06 46	.05 .06 48
25 N 113 W	.01 .01 1297	.01 .01 1257	.01 .01 1441	.01 .01 1409	.01 .01 1509	.01 .01 1467	.01 0.00 1508	0.00 .01 1431	.01 .01 1431	0.00 .01 1426	0.00 .01 1408	.01 .01 1269
25 N 114 W	.02 .04 147	.02 .04 128	.04 .05 139	.03 .05 150	.03 .04 176	.03 .03 206	.04 .04 177	.02 .02 225	.03 .04 200	.13 .06 185	.03 .04 149	.03 .03 125
25 N 115 W	.56 .65 31	.04 .09 32	.05 .08 42	.03 .08 59	.03 .07 86	.05 .08 66	.03 .04 81	.04 .04 73	.03 .06 67	.02 .04 66	.05 .05 46	.08 .09 30
25 N 116 W	.10 .17 15	.08 .06 22	.12 .13 27	.05 .12 23	.08 .08 35	.06 .09 31	.03 .05 46	.02 .03 53	.14 .08 44	.04 .11 25	.05 .06 37	.10 .16 14
25 N 117 W	.04 .07 23	.11 .10 27	.10 .12 30	.04 .09 35	.04 .06 52	.05 .06 40	.03 .05 51	.06 .06 59	.06 .08 38	.05 .07 45	.05 .08 34	.11 .16 22
25 N 118 W	.06 .06 33	.04 .10 29	.06 .10 34	.05 .20 41	.04 .08 61	.04 .06 58	.02 .05 67	.05 .07 57	.06 .10 48	.02 .05 61	.05 .08 42	.03 .08 50
25 N 119 W	.06 .08 52	.06 .10 34	.05 .07 50	.05 .14 42	.05 .08 54	.04 .07 70	.03 .07 58	.03 .05 59	.04 .09 56	.03 .05 58	.05 .11 49	.05 .06 48
25 N 120 W	.07 .09 37	.07 .12 36	.04 .06 49	.04 .08 52	.04 .07 61	.03 .05 44	.02 .04 55	.04 .06 51	.04 .07 41	.04 .06 45	.04 .09 54	.07 .08 36
25 N 121 W	.07 .06 46	.05 .10 42	.03 .06 53	.05 .07 38	.04 .06 49	.04 .06 41	.03 .06 55	.08 .08 46	.08 .08 41	.05 .05 60	.09 .15 33	.07 .07 37
25 N 122 W	.05 .08 50	.07 .08 52	.04 .06 56	.06 .08 59	.02 .05 68	.04 .05 36	.04 .06 44	.06 .06 45	.06 .09 48	.05 .06 54	.10 .06 49	.09 .06 56
26 N 113 W	.01 .02 372	.01 .02 399	.02 .02 424	.02 .02 397	.02 .02 444	.01 .02 452	.01 .06 398	.01 .01 408	.02 .02 428	.01 .02 427	.01 .02 439	.02 .02 389
26 N 114 W	.01 .01 1199	.01 .01 1201	.01 .01 1438	.01 .01 1327	.01 .01 1367	.01 .01 1334	.01 .01 1360	.01 .01 1346	.01 .01 1331	.02 .02 1333	.01 .01 1253	.01 .01 1165
26 N 115 W	.04 .04 120	.03 .04 115	.04 .05 126	.03 .05 117	.04 .04 135	.02 .04 158	.02 .03 148	.02 .03 150	.03 .05 147	.03 .04 129	.02 .04 129	.03 .05 96
26 N 116 W	.08 .09 30	.07 .14 24	.08 .10 34	.06 .10 45	.04 .07 65	.04 .07 68	.03 .04 68	.03 .05 59	.04 .07 66	.03 .05 55	.05 .08 60	.15 .80 30
26 N 117 W	.07 .16 16	.12 .18 15	.24 .28 16	.04 .09 33	.03 .07 30	.03 .09 37	.04 .05 59	.05 .08 48	.04 .09 42	.03 .06 35	.04 .05 30	.20 .19 16
26 N 118 W	.04 .09 32	.06 .09 24	.12 .12 32	.04 .15 26	.04 .08 35	.04 .07 34	.04 .05 35	.05 .06 43	.04 .07 52	.04 .07 39	.05 .10 25	.10 .14 13
26 N 119 W	.05 .09 33	.10 .11 29	.06 .09 26	.05 .14 33	.04 .08 41	.04 .08 36	.03 .06 43	.02 .08 38	.06 .10 24	.05 .07 30	.04 .07 37	.04 .09 27
26 N 120 W	.10 .07 30	.10 .15 24	.09 .15 34	.11 .09 38	.03 .08 57	.02 .05 59	.05 .08 50	.03 .06 45	.06 .09 48	.03 .06 57	.06 .06 43	.05 .09 38
26 N 121 W	.05 .07 59	.10 .12 26	.04 .10 40	.04 .09 54	.04 .09 55	.03 .06 69	.08 .08 43	.03 .05 66	.04 .09 47	.04 .05 51	.05 .14 42	.07 .08 46
26 N 122 W	.05 .06 37	.04 .06 52	.06 .06 61	.03 .09 54	.03 .07 55	.02 .04 57	.03 .05 60	.03 .05 57	.03 .06 60	.03 .04 63	.03 .05 70	.08 .07 50

LAT/LON	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
27 N 114 W	.02 .02 468	.02 .02 458	.02 .02 542	.02 .02 517	.02 .02 548	.02 .02 488	.01 .01 527	.01 .01 452	.02 .02 549	.01 .01 524	.02 .02 511	.02 .02 521
27 N 115 W	.01 .01 1113	.01 .01 1085	.01 .01 1245	.01 .01 1204	.01 .01 1250	.01 .01 1194	.01 .01 1209	.01 .01 1188	.01 .01 1169	.01 .01 1183	.01 .01 1122	.01 .02 973
27 N 116 W	.06 .07 76	.04 .06 102	.02 .10 88	.03 .04 108	.04 .05 101	.04 .05 110	.02 .04 99	.02 .03 120	.03 .06 130	.03 .06 84	.03 .05 86	.04 .07 62
27 N 117 W	.08 .12 29	.05 .07 34	.08 .10 43	.05 .11 48	.05 .08 51	.03 .06 64	.03 .06 71	.03 .06 71	.03 .05 76	.43 .73 55	.06 .07 51	.06 .10 25
27 N 118 W	.06 .10 28	.07 .16 20	.10 .14 23	.05 .11 32	.04 .08 36	.03 .06 43	.02 .05 70	.03 .04 53	.04 .08 49	.03 .04 31	.05 .09 37	.24 .10 19
27 N 119 W	.03 .09 19	.10 .32 12	.11 .08 16	.06 .09 34	.04 .10 32	.05 .10 32	.03 .10 29	.04 .05 32	.04 .07 37	.03 .06 37	.04 .05 26	.04 .22 20
27 N 120 W	.07 .11 34	.11 .27 19	.08 .11 23	.06 .11 20	.03 .14 30	.03 .08 33	.04 .07 29	.04 .07 38	.08 .09 36	.04 .09 26	.09 .14 17	.06 .08 15
27 N 121 W	.13 .09 40	.06 .05 25	.11 .12 29	.06 .12 42	.04 .08 46	.05 .10 18	.04 .12 31	.03 .05 49	.06 .13 24	.04 .07 49	.07 .07 33	.08 .14 17
27 N 122 W	.07 .06 36	.09 .12 33	.06 .11 51	.03 .10 53	.05 .08 58	.05 .06 64	.05 .09 54	.04 .08 62	.06 .09 48	.02 .05 75	.07 .08 53	.07 .05 62
27 N 123 W	.04 .07 69	.08 .09 52	.06 .09 63	.03 .07 75	.02 .05 93	.03 .06 90	.05 .08 60	.03 .05 80	.03 .04 91	.02 .04 105	.06 .08 77	.06 .09 51
28 N 115 W	. 3 .06 588	.02 .02 517	.01 .02 742	.02 .03 720	.01 .02 723	.01 .01 668	.01 .01 632	.01 .01 685	.01 .02 709	.01 .01 695	.01 .02 676	.02 .02 624
28 N 116 W	.01 .02 810	.01 .02 747	.01 .02 865	.01 .02 843	.01 .01 874	.01 .01 903	.01 .01 831	.01 .01 840	.01 .01 835	.01 .01 875	.01 .01 821	.02 .02 735
28 N 117 W	.06 .05 75	.05 .07 72	.05 .06 65	.03 .06 69	.04 .06 59	.03 .04 69	.04 .05 53	.03 .07 66	.04 .05 75	.04 .05 71	.04 .08 55	.09 .12 56
28 N 118 W	.05 .16 34	.07 .11 24	.05 .09 25	.07 .15 30	.05 .16 41	.03 .07 47	.02 .06 56	.04 .04 63	.04 .07 54	.02 .06 43	.05 .10 33	.05 .14 22
28 N 119 W	.06 .06 38	.04 .11 30	.05 .08 33	.05 .09 43	.04 .05 53	.04 .07 72	.03 .07 67	.03 .07 55	.04 .11 39	.03 .06 39	.06 .10 33	.13 .14 19
28 N 120 W	.20 .15 17	.29 .36 18	.08 .09 36	.06 .11 43	.06 .11 33	.03 .08 39	.06 .06 36	.04 .07 41	.03 .06 45	.05 .08 22	.05 .12 31	.10 .20 20
28 N 121 W	.06 .09 35	.08 .25 14	.08 .11 28	.05 .10 41	.04 .09 31	.05 .10 41	.05 .09 29	.02 .05 48	.04 .09 32	.04 .07 39	.03 .08 31	.06 .10 23
28 N 122 W	.06 .11 56	.04 .10 34	.07 .12 45	.05 .10 32	.05 .13 44	.05 .08 44	.03 .08 55	.05 .08 58	.03 .05 43	.03 .08 54	.08 .16 27	.05 .11 35
28 N 123 W	.10 .12 47	.08 .10 50	.06 .12 44	.03 .10 68	. 5 .06 70	.05 .11 37	.03 .10 41	.07 .07 65	.04 .05 65	.03 .04 80	.07 .09 75	.06 .06 58
28 N 124 W	.06 .08 48	.05 .07 46	.05 .12 43	.05 .09 44	.03 .07 65	.06 .06 54	.06 .09 46	.08 .07 47	.09 .08 38	.02 .04 88	.06 .07 67	.06 .09 51
29 N 115 W	.07 .09 62	.07 .08 88	.11 .09 90	.07 .09 80	.09 .10 71	.05 .06 66	.07 .07 61	.07 .04 63	.05 .07 59	.05 .05 58	.12 .07 73	.08 .09 67
29 N 116 W	.02 .01 1 30	.01 .01 1 49	.01 .01 1209	.01 .01 1155	.01 .01 1246	.01 .01 1080	.01 .01 1081	.01 .01 1115	.01 .01 1109	.01 .01 1112	.01 .01 1051	.01 .01 983
29 N 117 W	.03 .03 252	.02 .03 249	.02 .03 336	.02 .03 308	.02 .03 250	.02 .02 294	.02 .02 267	.01 .02 280	.02 .02 273	.02 .02 265	.02 .03 261	.03 .03 229
29 N 118 W	.03 .06 108	.08 .10 58	.07 .08 71	.07 .07 65	.05 .07 59	.04 .07 64	.05 .06 49	.03 .05 56	.08 .06 54	.04 .05 55	.05 .05 56	.06 .09 37
29 N 119 W	.07 .09 27	.07 .09 21	.10 .22 34	.05 .08 35	.05 .10 43	.04 .09 45	.03 .07 43	.05 .10 33	.04 .09 42	.02 .05 54	.10 .09 33	.05 .07 35
29 N 120 W	.06 .11 29	.07 .09 28	.10 .15 25	.05 .09 56	.04 .07 48	.04 .08 44	.05 .07 52	.03 .05 68	.04 .08 55	.06 .09 36	.06 .09 27	.06 .11 36
29 N 121 W	.05 .08 59	.11 .12 29	.09 .12 42	.05 .08 50	.05 .08 51	.03 .07 69	.04 .08 59	.03 .07 54	.07 .07 45	.04 .08 44	.46 1.27 42	.08 .09 34
29 N 122 W	.05 .10 73	.09 .13 48	.07 .13 51	.04 .10 56	.05 .06 81	.03 .06 84	.04 .09 52	.03 .06 86	.05 .06 44	.03 .06 82	.07 .07 62	.08 .08 39
29 N 123 W	.08 .12 63	.05 .13 39	.09 .11 39	.05 .12 45	.04 .07 65	.03 .08 61	.03 .06 65	.16 .07 61	.02 .05 73	.03 .06 68	.07 .09 54	.06 .09 58
29 N 124 W	.06 .11 51	.07 .07 50	.07 .14 36	.05 .08 50	.03 .07 76	.04 .07 54	.04 .10 54	.02 .05 57	.06 .05 53	.04 .06 80	.07 .08 89	.08 .11 31

LAT/LON	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
30 N 116 W	.02 .02 571	.02 .02 506	.02 .03 637	.01 .02 581	.01 .02 624	.01 .02 593	.01 .01 547	.01 .01 537	.01 .02 553	.01 .02 557	.01 .02 545	.01 .02 481
30 N 117 W	.01 .02 604	.01 .02 630	.01 .02 698	.01 .02 668	.05 .04 658	.01 .01 654	.01 .01 666	.01 .01 693	.01 .02 651	.01 .01 672	.03 .04 645	.02 .02 591
30 N 118 W	.04 .05 194	.02 .03 209	.03 .04 187	.04 .04 201	.03 .04 193	.03 .04 190	.02 .03 195	.02 .02 188	.02 .03 180	.02 .02 203	.03 .03 182	.04 .05 165
30 N 119 W	.07 .08 76	.06 .09 65	.07 .08 60	.04 .05 65	.10 .10 38	.04 .06 73	.02 .03 139	.03 .06 52	.05 .08 60	.06 .05 91	.06 .10 48	.08 .10 42
30 N 120 W	.05 .09 63	.05 .08 113	.08 .10 58	.05 .07 99	.03 .05 86	.05 .06 91	.04 .06 67	.05 .06 70	.04 .05 56	.04 .04 95	.07 .07 37	.06 .10 52
30 N 121 W	.07 .08 71	.06 .07 81	.07 .11 58	.04 .08 107	.03 .07 91	.04 .05 86	.03 .05 84	.03 .05 102	.04 .06 70	.03 .06 89	.04 .08 35	.10 .11 53
30 N 122 W	.05 .07 92	.12 .16 60	.09 .12 47	.08 .11 51	.04 .08 10[illegible]	.03 .08 104	.03 .06 77	.04 .06 88	.04 .07 73	.05 .06 74	.05 .08 51	.05 .09 49
30 N 123 W	.05 .08 78	.13 .13 50	.12 .15 48	.07 .14 54	.04 .06 87	.03 .07 80	.03 .06 72	.03 .12 73	.06 .09 69	.03 .09 82	.04 .10 69	.03 .05 96
30 N 124 W	.11 .11 66	.09 .11 80	.04 .07 55	.03 .07 75	.04 .07 110	.02 .05 108	.04 .08 60	.05 .07 83	.03 .07 66	.03 .07 113	.04 .09 87	.05 .09 63
30 N 125 W	.08 .12 78	.10 .15 66	.06 .10 57	.05 .10 65	.07 .08 55	.04 .08 78	.04 .08 64	.04 .08 78	.04 .06 70	.03 .07 86	.06 .09 72	.06 .08 65
31 N 117 W	.01 .01 776	.01 .02 793	.01 .01 922	.01 .01 880	.01 .01 916	.01 .01 866	.01 .01 826	.01 .01 837	.01 .01 861	.01 .01 821	.01 .02 793	.01 .02 706
31 N 118 W	.02 .03 394	.03 .03 402	.02 .03 446	.02 .02 442	.02 .03 441	.02 .02 384	.01 .02 360	.01 .01 443	.02 .02 499	.02 .02 441	.02 .02 459	.03 .03 372
31 N 119 W	.02 .03 294	.02 .04 294	.04 .06 236	.04 .04 286	.03 .03 253	.02 .03 296	.02 .03 255	.02 .03 214	.02 .03 267	.02 .02 345	.04 .04 222	.04 .05 154
31 N 120 W	.05 .07 159	.04 .06 143	.05 .07 131	.05 .06 149	.04 .06 144	.03 .05 124	.03 .05 158	.03 .04 126	.04 .06 98	.03 .03 212	.04 .07 122	.03 .06 84
31 N 121 W	.05 .08 153	.04 .08 145	.05 .10 101	.03 .06 131	.06 .06 119	.05 .07 105	.03 .04 132	.04 .05 95	.04 .08 78	.04 .05 131	.04 .06 101	.06 .08 78
31 N 122 W	.04 .06 115	.05 .10 98	.05 .10 97	.08 .11 70	.05 .07 104	.03 .07 104	.03 .05 106	.04 .06 87	.04 .09 79	.03 .08 127	.05 .10 107	.05 .08 87
31 N 123 W	.03 .06 171	.06 .10 110	.06 .08 84	.04 .10 91	.04 .06 109	.03 .07 123	.02 .05 170	.03 .05 142	.03 .06 133	.03 .07 153	.04 .06 111	.05 .10 79
31 N 124 W	.07 .09 112	.07 .12 86	.06 .10 105	.04 .07 173	.02 .04 207	.03 .06 169	.02 .05 166	.02 .06 102	.03 .06 133	.03 .05 146	.05 .08 119	.06 .10 107
31 N 125 W	.06 .08 134	.05 .09 121	.04 .07 139	.05 .08 144	.03 .06 126	.03 .06 150	.02 .04 160	.03 .07 125	.03 .06 124	.03 .08 166	.05 .09 122	.05 .11 92
31 N 126 W	.05 .08 157	.06 .10 137	.06 .07 152	.04 .07 145	.03 .05 149	.03 .05 155	.03 .06 158	.02 .05 145	.02 .04 144	.03 .06 180	.05 .06 148	.05 .09 131
32 N 117 W	.01 .01 [illegible]46	.01 .01 312	.01 .01 1055	.01 .01 967	.01 .01 1095	0.00 0.00 1059	0.00 0.00 931	0.00 0.00 1097	.01 .01 1041	.01 .01 1062	.01 .01 887	.01 .01 714
32 N 118 W	.01 .01 2163	.01 .01 1933	.01 .01 2268	.01 .01 2283	.01 0.00 2375	0.00 0.00 2221	.01 0.00 1934	0.00 0.00 2512	.01 0.00 2363	.01 .01 2284	.01 .01 1882	.01 .01 1133
32 N 119 W	.01 .02 1108	.02 .02 981	.02 .02 1244	.01 .02 1106	.01 .01 1140	.01 .01 1000	.01 .01 1054	.02 .01 1128	.01 .01 1220	.01 .01 1399	.02 .02 1017	.02 .02 768
32 N 120 W	.02 .03 451	.03 .05 350	.03 .03 491	.03 .04 479	.03 .03 465	.03 .04 354	.02 .02 500	.02 .02 433	.02 .02 573	.02 .03 492	.02 .03 419	.04 .05 252
32 N 121 W	.03 .06 241	.04 .06 252	.04 .07 235	.04 .05 249	.03 .05 254	.04 .05 196	.02 .04 272	.03 .04 225	.03 .04 245	.02 .04 293	.05 .06 233	.05 .07 189
32 N 122 W	.04 .07 198	.05 .08 214	.04 .08 212	.05 .08 214	.04 .06 188	.03 .06 190	.03 .05 229	.04 .06 171	.03 .05 191	.03 .04 302	.03 .05 208	.05 .08 176
32 N 123 W	.03 .06 287	.05 .08 197	.04 .07 218	.05 .08 198	.04 .07 190	.03 .07 172	.02 .04 203	.03 .05 188	.03 .05 181	.03 .06 253	.03 .06 232	.04 .08 184
32 N 124 W	.01 .04 771	.02 .04 531	.02 .03 630	.03 .05 432	.01 .04 569	.01 .03 551	.01 .02 662	.01 .02 711	.01 .02 662	.01 .04 828	.02 .03 623	.01 .03 637
32 N 125 W	.03 .05 302	.03 .06 273	.05 .06 289	.04 .05 267	.04 .05 273	.02 .05 263	.02 .05 268	.02 .04 284	.02 .04 237	.02 .05 353	.02 .04 323	.03 .06 363
32 N 126 W	.03 .05 289	.05 .07 252	.03 .05 307	.03 .05 300	.03 .05 278	.02 .04 257	.02 .05 267	.02 .04 280	.01 .04 247	.02 .05 320	.03 .04 352	.03 .06 311

LAT/LON	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
33 N 118 W	0.00 0.00 3638	.01 .01 3329	.01 0.00 3831	.01 0.00 3775	0.00 0.00 3805	0.00 0.00 3305	0.00 0.00 3107	0.00 0.00 3712	0.00 0.00 3483	0.00 0.00 3798	0.00 0.00 3536	.01 .01 2251
33 N 119 W	.01 .01 1351	.02 .02 1121	.02 .01 1557	.02 .01 1412	.02 .01 1492	.01 .01 1320	.01 .01 1079	.01 0.00 1595	.01 .01 1476	.01 .01 1686	.01 .01 1461	.02 .01 1023
33 N 120 W	.02 .02 966	.03 .04 610	.02 .02 930	.03 .02 935	.02 .02 1064	.02 .02 1124	.02 .02 823	.01 .02 967	.01 .02 1000	.01 .02 975	.02 .02 934	.03 .03 699
33 N 121 W	.02 .04 473	.03 .06 289	.04 .06 392	.04 .05 333	.05 .06 410	.03 .04 415	.03 .05 303	.02 .03 341	.03 .04 384	.03 .04 310	.03 .05 341	.03 .05 293
33 N 122 W	.03 .06 345	.04 .07 305	.04 .05 372	.04 .05 350	.03 .04 332	.04 .06 276	.04 .05 306	.02 .04 269	.02 .04 298	.03 .06 297	.03 .05 347	.03 .05 332
33 N 123 W	.03 .06 363	.03 .06 313	.04 .06 336	.02 .04 575	.02 .05 462	.03 .05 329	.02 .03 411	.02 .04 286	.02 .04 308	.02 .04 310	.03 .05 345	.03 .05 362
33 N 124 W	.02 .05 400	.03 .06 286	.03 .05 395	.04 .05 313	.02 .05 389	.03 .05 319	.02 .05 314	.01 .03 378	.02 .04 287	.02 .05 406	.03 .05 377	.03 .05 377
33 N 125 W	.03 .05 356	.03 .06 318	.03 .05 330	.03 .05 272	.02 .05 324	.03 .05 285	.02 .04 273	.01 .04 306	.02 .05 238	.02 .05 329	.03 .04 339	.03 .06 356
33 N 126 W	.06 .07 244	.04 .08 187	.04 .08 217	.04 .08 185	.02 .05 217	.03 .06 164	.02 .06 204	.03 .06 187	.02 .05 182	.02 .06 216	.03 .06 221	.03 .06 256
33 N 127 W	.05 .08 196	.05 .09 178	.04 .07 199	.07 .08 154	.03 .07 164	.04 .06 152	.03 .06 178	.03 .06 137	.03 .07 143	.03 .06 182	.05 .06 183	.06 .11 199
34 N 119 W	.01 .01 1565	.01 .01 1537	.01 0.00 1774	.01 0.00 1990	.01 .01 1924	0.00 0.00 1615	0.00 0.00 1623	0.00 0.00 1420	.01 0.00 1448	.01 0.00 1472	.01 .01 1261	.02 .01 995
34 N 120 W	.02 .02 599	.03 .03 588	.03 .02 743	.03 .03 705	.04 .03 643	.02 .02 721	.02 .02 775	.03 .02 650	.02 .02 656	.02 .02 640	.02 .02 652	.02 .02 769
34 N 121 W	.02 .03 576	.03 .04 506	.03 .04 594	.03 .04 535	.03 .04 543	.02 .03 676	.02 .03 603	.02 .02 650	.02 .03 577	.02 .03 567	.02 .03 558	.03 .04 495
34 N 122 W	.03 .05 276	.04 .07 261	.04 .07 274	.04 .07 239	.04 .06 258	.07 .09 265	.03 .04 284	.03 .04 232	.03 .05 246	.04 .07 228	.04 .08 272	.03 .05 256
34 N 123 W	.04 .07 230	.05 .08 228	.03 .08 258	.04 .07 185	.05 .08 189	.05 .08 190	.04 .06 197	.04 .06 156	.04 .05 172	.03 .07 263	.04 .06 207	.03 .07 212
34 N 124 W	.03 .05 265	.05 .07 204	.04 .07 229	.05 .07 218	.06 .08 147	.04 .07 166	.04 .08 152	.04 .06 146	.03 .13 188	.03 .06 273	.04 .07 206	.04 .07 241
34 N 125 W	.04 .06 229	.05 .08 199	.04 .07 240	.05 .07 204	.05 .08 152	.04 .07 143	.04 .07 149	.07 .07 137	.03 .06 175	.02 .07 234	.03 .05 217	.06 .09 234
34 N 126 W	.07 .08 206	.05 .09 200	.05 .07 204	.06 .09 195	.05 .09 149	.04 .08 132	.03 .07 141	.04 .07 101	.04 .06 142	.03 .06 189	.05 .08 184	.04 .07 232
34 N 127 W	.05 .08 208	.06 .07 182	.06 .07 212	.05 .08 185	.05 .08 138	.04 .07 134	.04 .08 122	.03 .08 96	.03 .08 145	.03 .06 164	.05 .08 187	.05 .06 218
34 N 128 W	.05 .08 230	.06 .08 184	.06 .07 224	.06 .09 182	.04 .07 179	.04 .07 148	.03 .06 127	.04 .06 129	.03 .07 130	.05 .06 169	.05 .08 186	.05 .07 215
35 N 121 W	.02 .03 525	.03 .04 477	.03 .04 613	.03 .04 572	.03 .03 586	.03 .04 551	.02 .02 631	.02 .03 564	.02 .02 536	.02 .03 658	.02 .03 559	.03 .04 447
35 N 122 W	.03 .05 296	.03 .05 310	.04 .05 376	.03 .05 388	.03 .04 432	.02 .04 480	.03 .04 441	.02 .03 445	.02 .03 418	.03 .04 422	.02 .04 423	.02 .05 274
35 N 123 W	.04 .07 243	.04 .08 218	.04 .07 224	.03 .06 284	.03 .06 276	.04 .06 296	.03 .04 293	.02 .06 325	.02 .04 306	.02 .04 262	.03 .06 283	.04 .08 211
35 N 124 W	.04 .08 222	.05 .09 202	.04 .08 186	.05 .08 189	.03 .06 243	.04 .06 229	.03 .06 225	.03 .05 243	.02 .04 204	.02 .05 279	.03 .06 237	.05 .09 202
35 N 125 W	.07 .12 207	.04 .07 178	.05 .08 171	.05 .09 165	.05 .09 161	.04 .07 200	.03 .06 177	.03 .06 174	.04 .07 174	.03 .07 187	.03 .06 207	.06 .10 169
35 N 126 W	.06 .12 189	.07 .10 147	.05 .12 157	.04 .10 183	.06 .08 141	.04 .08 134	.04 .08 138	.04 .06 147	.04 .07 139	.04 .08 174	.04 .08 179	.06 .08 184
35 N 127 W	.05 .09 193	.05 .08 181	.06 .08 198	.05 .08 171	.04 .09 153	.05 .07 154	.04 .08 129	.03 .06 150	.03 .07 111	.05 .08 206	.05 .09 191	.05 .09 201
35 N 128 W	.04 .06 366	.05 .07 317	.04 .06 373	.05 .05 259	.03 .05 270	.02 .06 243	.02 .05 313	.02 .04 316	.03 .06 273	.02 .05 356	.03 .05 370	.05 .06 368
35 N 129 W	.04 .06 400	.05 .06 394	.03 .05 479	.04 .05 379	.02 .04 352	.02 .04 337	.02 .04 312	.02 .03 326	.02 .05 324	.03 .05 404	.03 .05 373	.04 .05 411
35 N 130 W	.04 .05 568	.04 .05 523	.03 .05 577	.04 .04 487	.02 .04 492	.02 .03 442	.02 .04 464	.01 .03 446	.02 .04 476	.02 .04 592	.03 .04 554	.03 .05 562

LAT/LON	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
36 N 122 W	.02 .04 552	.03 .05 465	.03 .04 592	.02 .04 621	.03 .04 631	.02 .03 759	.02 .03 767	.02 .03 561	.02 .03 604	.02 .04 553	.02 .03 561	.03 .04 411
36 N 123 W	.03 .06 286	.04 .06 342	.03 .06 298	.03 .07 364	.02 .04 468	.02 .04 591	.02 .04 577	.02 .03 525	.02 .03 478	.02 .05 418	.03 .05 380	.04 .09 247
36 N 124 W	.05 .08 240	.03 .08 228	.04 .06 215	.03 .07 279	.03 .05 360	.03 .05 351	.03 .05 339	.02 .04 360	.03 .05 286	.02 .06 269	.03 .06 257	.04 .06 246
36 N 125 W	.05 .08 296	.04 .09 206	.04 .07 225	.04 .08 271	.04 .06 281	.03 .06 298	.03 .06 297	.03 .05 291	.02 .07 258	.03 .07 250	.03 .06 270	.04 .07 255
36 N 126 W	.04 .08 446	.03 .06 414	.03 .06 449	.03 .05 368	.03 .05 371	.03 .06 357	.02 .05 358	.02 .04 382	.02 .06 352	.03 .06 398	.02 .05 530	.04 .07 397
36 N 127 W	.02 .04 899	.03 .05 748	.03 .04 694	.02 .04 624	.02 .04 651	.02 .04 655	.02 .04 584	.01 .03 714	.02 .04 646	.02 .04 699	.02 .04 660	.02 .05 734
36 N 128 W	.02 .04 1060	.03 .04 975	.02 .03 963	.02 .03 855	.01 .03 769	.01 .03 868	.01 .03 861	.01 .02 952	.01 .04 929	.02 .03 913	.02 .03 1168	.02 .03 397
36 N 129 W	.04 .05 519	.04 .05 511	.03 .04 682	.03 .04 616	.02 .04 566	.02 .04 581	.01 .03 552	.01 .03 585	.01 .03 637	.03 .04 612	.03 .04 598	.04 .06 620
36 N 130 W	.06 .08 303	.06 .06 315	.04 .06 382	.05 .06 331	.03 .06 274	.02 .05 298	.02 .05 249	.02 .04 259	.04 .05 299	.03 .04 373	.04 .05 404	.06 .07 322
36 N 131 W	.08 .09 235	.08 .08 266	.06 .08 272	.05 .07 238	.04 .06 212	.04 .05 209	.03 .05 138	.03 .05 185	.04 .06 191	.04 .06 250	.06 .08 251	.07 .08 234
37 N 122 W	.03 .05 412	.03 .05 337	.03 .04 343	.03 .04 378	.03 .04 432	.03 .04 391	.01 .02 581	.02 .03 354	.02 .03 400	.02 .03 433	.02 .04 376	.03 .05 325
37 N 123 W	.03 .05 588	.03 .06 591	.04 .05 688	.03 .05 672	.03 .04 738	.02 .03 998	.02 .02 881	.01 .03 836	.01 .02 882	.02 .04 797	.03 .04 687	.04 .06 637
37 N 124 W	.04 .07 578	.04 .06 572	.03 .05 605	.03 .05 514	.04 .06 564	.03 .05 570	.03 .04 523	.02 .04 537	.02 .04 533	.03 .05 602	.02 .04 645	.03 .05 534
37 N 125 W	.02 .05 731	.03 .05 586	.02 .04 789	.02 .05 719	.02 .04 748	.02 .04 696	.02 .03 706	.02 .03 681	.02 .04 664	.02 .04 755	.02 .04 883	.02 .05 688
37 N 126 W	.03 .05 633	.02 .05 545	.02 .05 696	.02 .05 703	.02 .05 685	.02 .04 720	.02 .04 684	.01 .03 603	.02 .04 602	.01 .04 651	.02 .04 722	.02 .05 617
37 N 127 W	.04 .06 435	.04 .08 391	.03 .06 424	.03 .05 473	.02 .05 532	.02 .06 447	.02 .05 438	.02 .05 406	.02 .05 453	.02 .05 528	.04 .05 489	.03 .07 430
37 N 128 W	.06 .08 313	.06 .08 299	.04 .07 352	.03 .06 343	.02 .05 369	.02 .05 361	.03 .06 286	.02 .06 274	.02 .06 405	.02 .05 410	.04 .06 357	.06 .07 337
37 N 129 W	.06 .08 263	.06 .08 236	.06 .09 279	.04 .06 322	.04 .06 306	.03 .06 331	.02 .06 253	.02 .05 283	.02 .05 333	.03 .05 387	.04 .06 351	.06 .09 271
37 N 130 W	.06 .09 233	.06 .08 230	.05 .08 243	.04 .07 312	.04 .05 281	.02 .05 306	.02 .05 271	.03 .05 261	.03 .05 345	.03 .05 338	.05 .06 298	.06 .10 257
37 N 131 W	.07 .09 223	.07 .10 201	.08 .10 209	.05 .05 265	.04 .05 229	.04 .06 239	.02 .05 234	.02 .04 242	.03 .05 262	.04 .05 291	.05 .07 266	.07 .08 254
38 N 123 W	.02 .03 956	.02 .03 919	.03 .03 937	.03 .03 1139	.02 .03 1121	.03 .03 1034	.01 .02 1132	.02 .02 931	.01 .02 1025	.01 .03 986	.02 .03 827	.03 .03 791
38 N 124 W	.04 .09 319	.04 .08 332	.04 .06 351	.03 .05 464	.04 .06 459	.03 .05 568	.03 .05 560	.02 .04 563	.02 .04 533	.03 .04 423	.03 .05 530	.04 .07 453
38 N 125 W	.05 .09 208	.05 .10 222	.05 .12 216	.04 .08 296	.04 .09 274	.04 .07 315	.03 .06 338	.03 .05 370	.03 .07 327	.03 .07 287	.03 .06 289	.05 .09 222
38 N 126 W	.08 .14 162	.04 .11 229	.05 .09 191	.04 .10 216	.03 .08 259	.03 .08 248	.04 .06 292	.03 .05 340	.03 .06 300	.03 .09 272	.06 .08 239	.07 .12 211
38 N 127 W	.07 .17 175	.07 .11 176	.05 .08 233	.04 .08 243	.02 .07 318	.03 .06 338	.03 .06 384	.03 .06 349	.03 .06 318	.03 .08 285	.04 .06 266	.08 .11 214
38 N 128 W	.06 .13 206	.09 .12 193	.04 .07 261	.04 .07 277	.03 .05 383	.02 .06 381	.02 .05 449	.02 .04 435	.02 .05 416	.04 .07 300	.05 .07 282	.07 .09 239
38 N 129 W	.08 .13 177	.06 .1[illegible] 206	.06 .09 214	.05 .05 247	.03 .05 307	.02 .09 330	.02 .05 355	.02 .05 337	.03 .05 320	.03 .07 249	.05 .06 253	.08 .09 217
38 N 130 W	.09 .15 140	.12 .11 172	.07 .10 170	.06 .08 180	.03 .06 247	.03 .05 258	.03 .05 273	.02 .04 281	.03 .05 272	.05 .08 192	.08 .09 206	.10 .10 196
38 N 131 W	.09 .13 160	.08 .12 146	.07 .12 151	.07 .09 151	.03 .05 248	.04 .08 201	.03 .05 232	.02 .04 291	.04 .06 221	.06 .08 198	.07 .08 174	.08 .12 190
38 N 132 W	.11 .17 126	.13 .12 139	.08 .08 166	.07 .09 145	.05 .07 189	.04 .06 181	.03 .05 208	.06 .05 225	.04 .04 238	.08 .08 193	.07 .08 178	.11 .12 157

LAT/LON	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
39 N	.04	.04	.03	.04	.05	.04	.03	.03	.03	.02	.03	.09
124 W	.08	.07	.06	.06	.08	.06	.07	.05	.05	.05	.05	.12
	337	393	392	437	423	496	465	415	420	406	422	344
39 N	.10	.06	.08	.05	.05	.05	.04	.04	.04	.04	.05	.05
125 W	.12	.10	.15	.10	.10	.10	.08	.08	.09	.08	.12	.12
	181	171	162	202	229	273	311	267	242	218	157	158
39 N	.07	.09	.07	.04	.04	.03	.03	.03	.03	.07	.06	.08
126 W	.17	.11	.11	.09	.09	.07	.06	.07	.07	.17	.09	.13
	172	160	165	231	232	301	331	318	269	220	206	155
39 N	.09	.06	.07	.05	.05	.05	.04	.03	.04	.05	.08	.08
127 W	.17	.09	.13	.10	.10	.10	.08	.07	.09	.12	.10	.13
	134	173	167	213	173	182	222	244	196	197	174	141
39 N	.07	.10	.07	.06	.04	.04	.03	.03	.03	.05	.07	.08
128 W	.14	.11	.13	.11	.10	.09	.07	.07	.07	.10	.20	.11
	138	135	159	164	161	167	233	219	227	171	163	136
39 N	.07	.10	.07	.05	.04	.03	.02	.03	.03	.06	.06	.07
129 W	.11	.10	.10	.09	.06	.06	.06	.06	.07	.09	.09	.09
	133	162	202	229	249	254	288	248	238	178	184	172
39 N	.07	.07	.05	.03	.03	.02	.02	.02	.03	.06	.07	.05
130 W	.08	.07	.07	.07	.04	.04	.05	.05	.06	.10	.09	.07
	304	337	248	349	451	339	356	324	251	239	187	335
39 N	.13	.11	.05	.04	.04	.03	.02	.02	.04	.06	.09	.08
131 W	.13	.13	.08	.05	.04	.05	.04	.03	.07	.08	.09	.10
	138	149	192	215	347	264	400	357	284	187	198	174
39 N	.10	.13	.10	.06	.05	.04	.02	.03	.04	.04	.09	.13
132 W	.12	.15	.12	.08	.07	.05	.04	.06	.06	.07	.10	.14
	135	101	157	163	185	251	269	219	235	159	172	148
39 N	.12	.10	.08	.06	.05	.03	.03	.03	.04	.05	.09	.08
133 W	.18	.21	.11	.11	.08	.05	.04	.05	.04	.06	.08	.11
	132	112	145	143	162	206	240	186	246	316	220	150
40 N	.03	.03	.03	.02	.02	.02	.03	.05	.02	.02	.02	.04
124 W	.09	.06	.07	.05	.05	.04	.05	.06	.04	.06	.07	.08
	727	710	747	736	853	605	658	517	478	490	525	454
40 N	.07	.07	.05	.04	.05	.04	.05	.04	.04	.03	.05	.07
125 W	.15	.14	.11	.11	.12	.09	.09	.09	.11	.12	.11	.15
	178	168	184	210	167	223	212	233	193	191	213	151
40 N	.09	.06	.11	.05	.10	.06	.05	.04	.05	.06	.07	.09
126 W	.18	.28	.19	.13	.14	.17	.12	.11	.13	.13	.17	.23
	111	75	80	102	124	105	127	127	95	114	128	101
40 N	.09	.09	.13	.05	.04	.03	.04	.03	.04	.05	.07	.08
127 W	.14	.13	.16	.11	.09	.08	.09	.06	.09	.12	.16	.13
	127	122	115	165	167	196	204	270	162	169	122	123
40 N	.06	.09	.10	.05	.03	.03	.02	.03	.04	.05	.08	.08
128 W	.12	.14	.11	.09	.08	.21	.07	.06	.08	.09	.12	.09
	287	162	153	212	201	248	301	247	205	190	136	225
40 N	.07	.06	.05	.05	.04	.03	.03	.04	.05	.04	.08	.07
129 W	.10	.11	.07	.07	.05	.06	.05	.06	.08	.08	.09	.11
	167	189	276	305	279	230	268	249	243	253	218	158
40 N	.07	.06	.05	.04	.03	.02	.02	.02	.04	.04	.05	.05
130 W	.08	.07	.05	.05	.04	.04	.05	.06	.06	.05	.06	.08
	209	295	568	479	519	519	499	393	359	472	396	197
40 N	.10	.11	.08	.07	.05	.03	.04	.02	.05	.07	.08	.11
131 W	.15	.12	.10	.08	.15	.06	.05	.04	.06	.07	.10	.12
	108	156	145	168	191	185	216	245	170	147	153	129
40 N	.11	.10	.08	.05	.05	.02	.02	.02	.04	.13	.08	.10
132 W	.10	.09	.10	.07	.06	.04	.04	.03	.05	.08	.09	.13
	165	162	182	183	232	261	304	271	233	213	177	173
40 N	.09	.17	.08	.04	.04	.02	.02	.02	.03	.11	.08	.09
133 W	.11	.09	.08	.06	.05	.03	.03	.04	.04	.06	.07	.11
	172	166	226	291	268	384	375	341	429	362	235	203
41 N	.08	.04	.05	.05	.05	.04	.08	.02	.02	.03	.04	.07
124 W	.17	.10	.12	.21	.12	.11	.14	.06	.06	.06	.08	.07
	102	112	101	114	125	120	114	180	208	212	209	178
41 N	.06	.05	.03	.03	.03	.03	.04	.03	.03	.04	.03	.11
125 W	.16	.14	.09	.11	.10	.09	.09	.08	.10	.11	.11	.17
	204	227	256	225	243	258	271	236	236	271	246	192
41 N	.17	.09	.12	.08	.04	.05	.12	.06	.04	.08	.05	.10
126 W	.16	.19	.29	.15	.16	.14	.29	.14	.18	.27	.15	.19
	77	77	82	93	102	87	84	87	91	118	101	98
41 N	.12	.16	.16	.12	.04	.08	.07	.06	.09	.07	.11	.14
127 W	.22	.17	.26	.17	.10	.18	.14	.12	.20	.15	.19	.21
	88	84	79	117	105	66	64	85	60	82	94	84
41 N	.29	.13	.20	.06	.08	.06	.04	.04	.05	.08	.16	.14
128 W	.25	.14	.36	.09	.13	.13	.13	.14	.12	.12	.24	.14
	77	60	66	101	69	76	83	77	65	89	83	86
41 N	.13	.12	.50	.05	.06	.03	.03	.05	.04	.09	.10	.20
129 W	.18	.18	.43	.08	.09	.06	.07	.07	.09	.11	.12	.14
	103	97	108	120	119	154	137	122	118	111	107	113
41 N	.18	.11	.11	.04	.04	.03	.02	.02	.05	.08	.08	.10
130 W	.14	.16	.09	.05	.06	.05	.05	.05	.06	.08	.10	.15
	113	156	164	216	218	274	253	295	199	206	154	122
41 N	.09	.12	.09	.05	.04	.02	.05	.03	.04	.05	.08	.09
131 W	.12	.16	.10	.06	.06	.04	.11	.03	.05	.08	.12	.11
	175	202	221	289	268	270	344	341	247	227	195	161
41 N	.10	.14	.10	.08	.08	.05	.03	.04	.06	.09	.12	.12
132 W	.12	.18	.12	.09	.09	.05	.05	.07	.07	.08	.11	.17
	116	113	115	155	161	161	171	152	148	162	139	131
41 N	.12	.12	.13	.07	.08	.04	.04	.03	.05	.08	.15	.10
133 W	.16	.18	.16	.09	.08	.05	.26	.05	.07	.11	.12	.13
	117	99	115	133	118	157	152	168	141	137	113	123

LAT/LON	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
42 N 124 W	.08 .15 103	.06 .14 107	.06 .12 74	.05 .15 92	.05 .13 96	.05 .09 112	.05 .13 128	.05 .13 90	.03 .10 112	.02 .09 112	.07 .17 88	.06 .12 76
42 N 125 W	.06 .12 221	.06 .11 241	.04 .08 273	.03 .11 259	.04 .14 214	.03 .10 303	.03 .09 296	.03 .09 238	.03 .10 243	.03 .08 268	.03 .10 272	.06 .15 196
42 N 126 W	.17 .28 73	.15 .25 60	.15 .21 77	.08 .14 80	.08 .15 75	.06 .13 61	.07 .17 63	.04 .12 76	.08 .21 50	.10 .23 73	.09 .15 77	.17 .23 58
42 N 127 W	.18 .21 86	.09 .17 82	.18 .23 95	.10 .21 89	.05 .09 83	.07 .11 73	.08 .12 72	.06 .11 64	.08 .18 69	.11 .15 94	.12 .15 114	.14 .16 102
42 N 128 W	.24 .2 94	.10 .18 64	.23 .24 87	.10 .13 68	.07 .14 70	.10 .25 67	.06 .15 67	.07 .18 61	.09 .11 53	.08 .13 82	.14 .25 86	.16 .20 110
42 N 129 W	.12 .16 212	.10 .13 166	.06 .09 260	.06 .07 244	.06 .07 241	.04 .07 157	.04 .06 143	.02 .05 264	.11 .13 48	.14 .19 61	.11 .13 152	.10 .11 257
42 N 130 W	.10 .14 146	.14 .17 142	.12 .12 124	.07 .09 93	.05 .09 100	.04 .07 139	.04 .09 128	.32 .39 100	.21 .09 52	.12 .12 76	.12 .1 137	.14 .19 114
42 N 131 W	.07 .09 187	.14 .13 158	.07 .10 199	.07 .05 216	.05 .07 160	.04 .05 183	.03 .04 280	.02 .04 288	.05 .07 206	.10 .09 166	.10 .13 158	.13 .12 138
42 N 132 W	.13 .17 121	.11 .18 120	.15 .13 123	.08 .09 185	.05 .05 194	.04 .05 228	.03 .05 249	.04 .05 234	.04 .06 190	.08 .09 159	.12 .19 116	.12 .21 126
42 N 133 W	.15 .15 144	.16 .18 110	.13 .10 167	.07 .09 181	.06 .07 256	.05 .08 257	.03 .04 233	.03 .03 259	.04 .05 219	.08 .07 200	.15 .17 119	.12 .15 139
43 N 124 W	.11 .14 95	.09 .11 102	.06 .12 80	.03 .12 84	.06 .10 87	.03 .07 104	.03 .10 92	.03 .09 76	.02 .06 123	.02 .08 103	.08 .21 72	.07 .13 104
43 N 125 W	.06 .13 254	.04 .13 272	.06 .10 255	.03 .09 241	.03 .09 241	.02 .07 280	.02 .06 304	.02 .06 213	.02 .09 281	.10 .07 456	.04 .09 423	.06 .15 224
43 N 126 W	.13 .19 71	.13 .22 58	.15 .14 61	.13 .12 59	.06 .14 59	.06 .17 41	.07 .16 42	.03 .17 52	.07 .21 47	.07 .12 87	.13 .15 77	.12 .23 68
43 N 127 W	.24 .33 71	.13 .22 64	.12 .20 84	.10 .18 64	.06 .09 64	.06 .13 48	.04 .10 58	.11 .17 54	.07 .14 53	.09 .13 105	.11 .15 110	.20 .25 83
43 N 128 W	.18 .21 85	.23 .31 78	.30 .22 75	.11 .14 68	.06 .11 69	.04 .08 64	.09 .11 64	.05 .08 54	.07 .12 71	.09 .17 88	.14 .15 104	.16 .22 105
43 N 129 W	.14 .17 136	.16 .21 98	.14 .15 123	.09 .13 93	.12 .13 97	.09 .23 87	.05 .08 76	.05 .10 86	.07 .08 77	.12 .17 82	.15 .18 105	.13 .23 107
43 N 130 W	.08 .10 330	.08 .12 156	.08 .10 306	.05 .08 317	.03 .05 346	.02 .05 369	.02 .05 320	.02 .04 330	.03 .05 288	.09 .10 173	.12 .12 118	.07 .10 332
43 N 131 W	.12 .15 119	.10 .14 149	.11 .11 139	.11 .14 117	.05 .10 133	.04 .05 159	.04 .06 156	.02 .05 169	.06 .09 126	.10 .09 130	.11 .12 116	.19 .22 103
43 N 132 W	.15 .19 99	.12 .26 101	.13 .15 114	.11 .16 95	.10 .09 85	.07 .08 83	.05 .07 94	.05 .08 84	.08 .10 75	.14 .12 81	.19 .20 78	.17 .22 79
43 N 133 W	.14 .13 127	.12 .17 112	.09 .10 117	.09 .09 147	.08 .09 122	.04 .06 128	.04 .05 115	.06 .05 129	.07 .07 100	.09 .12 149	.13 .12 143	.20 .47 121
44 N 124 W	.09 .17 126	.08 .10 133	.09 .16 118	.04 .08 136	.03 .06 162	.01 .07 133	.02 .05 161	.01 .05 95	.03 .05 138	.03 .08 156	.04 .09 174	.11 .16 94
44 N 125 W	.07 .14 229	.05 .10 252	.05 .09 305	.03 .08 237	.06 .07 259	.02 .06 271	.01 .05 341	.01 .05 286	.01 .04 540	.02 .07 492	.03 .06 437	.08 .18 221
44 N 126 W	.17 .23 84	.14 .25 45	.09 .16 68	.18 .65 52	.06 .10 73	.05 .12 63	.05 .17 61	.02 .09 76	.10 .24 39	.16 .19 80	.09 .13 76	.17 .32 65
44 N 127 W	.20 .28 75	.20 .23 62	.13 .21 77	.14 .17 55	.08 .12 77	.08 .11 55	.05 .15 42	.04 .09 64	.10 .12 61	.13 .16 77	.09 .14 103	.17 .30 81
44 N 128 W	.19 .22 99	.16 .23 124	.15 .17 103	.10 .10 90	.06 .11 109	.27 .47 83	.05 .11 79	.05 .08 74	.05 .10 124	.05 .07 288	.07 .12 270	.25 .22 103
44 N 129 W	.15 .18 99	.14 .17 94	.16 .17 115	.10 .13 125	.07 .06 102	.05 .11 107	.04 .07 104	.04 .08 94	.05 .08 119	.07 .11 168	.16 .12 145	.18 .22 139
44 N 130 W	.10 .14 134	.11 .15 116	.16 .16 126	.10 .16 102	.09 .14 110	.07 .20 110	.04 .09 110	.06 .09 91	.05 .09 113	.09 .14 125	.13 .20 117	.16 .19 117
44 N 131 W	.10 .12 231	.09 .10 194	.07 .07 318	.05 .06 256	.04 .06 288	.02 .04 417	.02 .04 384	.05 .03 385	.03 .05 381	.04 .07 372	.06 .08 273	.13 .14 238
44 N 132 W	.12 .14 170	.11 .17 150	.11 .11 167	.07 .07 181	.06 .08 177	.05 .06 169	.03 .05 175	.03 .05 149	.05 .08 143	.08 .10 173	.13 .12 151	.11 .17 177
44 N 133 W	.14 .16 137	.15 .16 133	.13 .12 118	.12 .11 101	.07 .07 105	.08 .07 110	.06 .06 108	.04 .07 109	.07 .10 100	.11 .10 137	.13 .14 116	.11 .15 135

LAT/LON	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
45 N 124 W	.11 .12 175	.06 .08 188	.06 .09 164	.04 .09 150	.04 .06 219	.01 .04 230	.01 .05 204	.01 .04 182	.02 .07 161	.04 .07 211	.10 .12 175	.11 .14 141
45 N 125 W	.06 .10 277	.04 .08 338	.06 .10 329	.04 .06 277	.03 .05 344	.01 .05 349	.01 .04 368	.01 .04 238	.01 .03 422	.03 .06 458	.05 .10 355	.10 .14 233
45 N 126 W	.13 .24 109	.08 .12 116	.14 .18 83	.07 .15 87	.05 .08 103	.03 .08 129	.05 .13 87	.05 .08 96	.09 .12 99	.14 .10 115	.11 .16 113	.18 .27 101
45 N 127 W	.19 .26 98	.14 .17 101	.12 .17 115	.09 .18 82	.06 .11 104	.05 .08 75	.06 .11 81	.04 .07 81	.06 .12 72	.12 .12 110	.11 .15 132	.20 .29 86
45 N 128 W	.11 .20 102	.13 .14 99	.10 .15 113	.09 .21 105	.04 .04 297	.05 .07 100	.05 .08 79	.03 .07 147	.07 .11 71	.17 .15 113	.14 .13 121	.29 .27 85
45 N 129 W	.14 .19 119	.13 .13 97	.11 .16 144	.08 .10 109	.06 .09 100	.05 .07 115	.05 .08 97	.04 .07 95	.08 .08 123	.19 .14 117	.12 .18 131	.11 .16 109
45 N 130 W	.06 .07 507	.06 .08 500	.05 .05 539	.04 .05 554	.03 .05 386	.03 .03 420	.01 .04 559	.03 .03 307	.03 .03 471	.06 .06 379	.07 .09 482	.08 .10 425
45 N 131 W	.08 .10 257	.09 .10 273	.07 .07 284	.05 .07 223	.04 .06 260	.03 .04 251	.09 .04 274	.03 .05 222	.05 .07 209	.07 .08 216	.10 .12 199	.11 .12 255
45 N 132 W	.12 .17 166	.12 .12 143	.11 .10 163	.08 .08 192	.07 .07 170	.04 .06 167	.05 .06 129	.05 .06 141	.06 .08 145	.10 .11 160	.09 .13 132	.18 .16 127
45 N 133 W	.23 .29 61	.29 .25 53	.23 .22 59	.15 .16 59	.16 .12 55	.07 .09 68	.08 .08 56	.09 .12 45	.07 .09 56	.13 .15 93	.16 .18 79	.25 .34 75
46 N 124 W	.04 .04 907	.04 .06 660	.03 .07 692	.03 .05 694	.03 .04 709	.02 .03 712	.01 .02 771	.01 .02 696	.02 .03 724	.03 .05 818	.04 .06 719	.06 .08 675
46 N 125 W	.09 .10 220	.07 .10 222	.08 .08 269	.05 .09 204	.03 .05 246	.02 .04 291	.02 .04 314	.01 .04 255	.04 .06 269	.07 .09 285	.07 .12 258	.13 .14 154
46 N 126 W	.13 .19 100	.13 .19 93	.18 .17 84	.09 .13 74	.06 .10 82	.07 .13 78	.04 .08 95	.04 .08 87	.19 .16 88	.11 .27 89	.24 .27 115	.27 .21 76
46 N 127 W	.14 .16 126	.11 .13 120	.11 .14 140	.08 .11 108	.05 .05 100	.07 .10 96	.05 .09 102	.03 .06 98	.06 .11 95	.15 .15 105	.12 .14 181	.18 .15 114
46 N 128 W	.12 .17 139	.16 .15 148	.10 .11 164	.06 .10 118	.07 .08 109	.05 .08 106	.04 .08 113	.05 .06 110	.06 .07 118	.11 .12 139	.14 .17 145	.12 .13 145
46 N 129 W	.16 .17 145	.13 .16 136	.12 .11 154	.15 .11 129	.05 .09 116	.05 .06 115	.05 .06 107	.04 .05 120	.05 .09 113	.10 .14 133	.10 .12 136	.13 .18 145
46 N 130 W	.11 .14 131	.14 .16 130	.11 .12 152	.15 .12 123	.06 .06 120	.06 .08 140	.05 .07 114	.05 .08 98	.09 .12 102	.14 .11 123	.12 .12 137	.13 .16 130
46 N 131 W	.14 .15 141	.12 .16 107	.11 .15 112	.07 .10 158	.05 .08 157	.04 .05 142	.04 .07 123	.05 .05 144	.08 .08 141	.13 .13 125	.15 .17 154	.12 .12 148
46 N 132 W	.10 .10 240	.09 .09 182	.09 .08 254	.08 .08 295	.03 .05 229	.06 .06 145	.14 .12 138	.06 .08 121	.07 .08 151	.09 .12 121	.13 .14 114	.16 .17 134
46 N 133 W	.15 .14 106	.17 .20 92	.15 .15 83	.12 .12 95	.14 .14 92	.07 .08 77	.06 .09 74	.05 .06 86	.10 .13 90	.13 .12 105	.17 .18 91	.24 .23 108
47 N 124 W	.18 .15 80	.10 .11 96	.07 .10 81	.08 .10 83	.04 .09 84	.02 .03 117	.02 .03 119	.02 .04 80	.03 .04 101	.10 .06 102	.07 .09 173	.18 .19 74
47 N 125 W	.10 .12 228	.08 .10 198	.06 .08 252	.07 .09 195	.04 .05 197	.02 .03 356	.01 .02 450	.01 .02 436	.03 .03 274	.04 .17 357	.07 .09 304	.11 .15 155
47 N 126 W	.14 .16 196	.12 .13 158	.10 .11 177	.09 .10 185	.05 .08 174	.06 .08 152	.03 .06 143	.03 .06 174	.09 .10 157	.09 .11 192	.10 .11 223	.12 .14 138
47 N 127 W	.15 .13 171	.10 .12 177	.11 .09 215	.08 .12 171	.05 .08 177	.08 .11 175	.03 .06 149	.05 .06 151	.08 .10 181	.07 .10 170	.11 .13 186	.14 .13 159
47 N 128 W	.15 .12 151	.16 .19 127	.09 .12 156	.10 .13 130	.06 .06 128	.09 .12 119	.08 .06 108	.04 .08 116	.06 .10 183	.08 .09 293	.10 .19 154	.15 .17 125
47 N 129 W	.19 .18 88	.21 .20 100	.13 .16 83	.09 .13 94	.06 .06 99	.06 .08 95	.04 .07 94	.05 .08 86	.08 .09 107	.09 .10 198	.11 .16 115	.16 .18 98
47 N 130 W	.10 .12 262	.10 .12 283	.10 .09 299	.05 .06 276	.05 .05 213	.03 .06 247	.02 .03 270	.02 .05 242	.07 .06 257	.13 .14 148	.19 .21 78	.09 .08 282
47 N 131 W	.08 .13 237	.12 .16 120	.08 .09 180	.06 .08 200	.04 .07 198	.03 .04 267	.03 .04 237	.03 .05 316	.04 .06 326	.11 .11 202	.10 .14 185	.10 .12 262
47 N 132 W	.11 .16 159	.08 .11 206	.09 .10 171	.13 .09 157	.04 .06 265	.03 .03 374	.03 .04 292	.04 .05 259	.04 .06 232	.08 .10 257	.08 .10 248	.11 .17 196
47 N 133 W	.16 .17 77	.18 .19 84	.19 .15 79	.11 .17 88	.10 .14 76	.08 .11 76	.07 .08 61	.06 .10 85	.08 .15 96	.11 .12 114	.20 .22 90	.18 .17 91

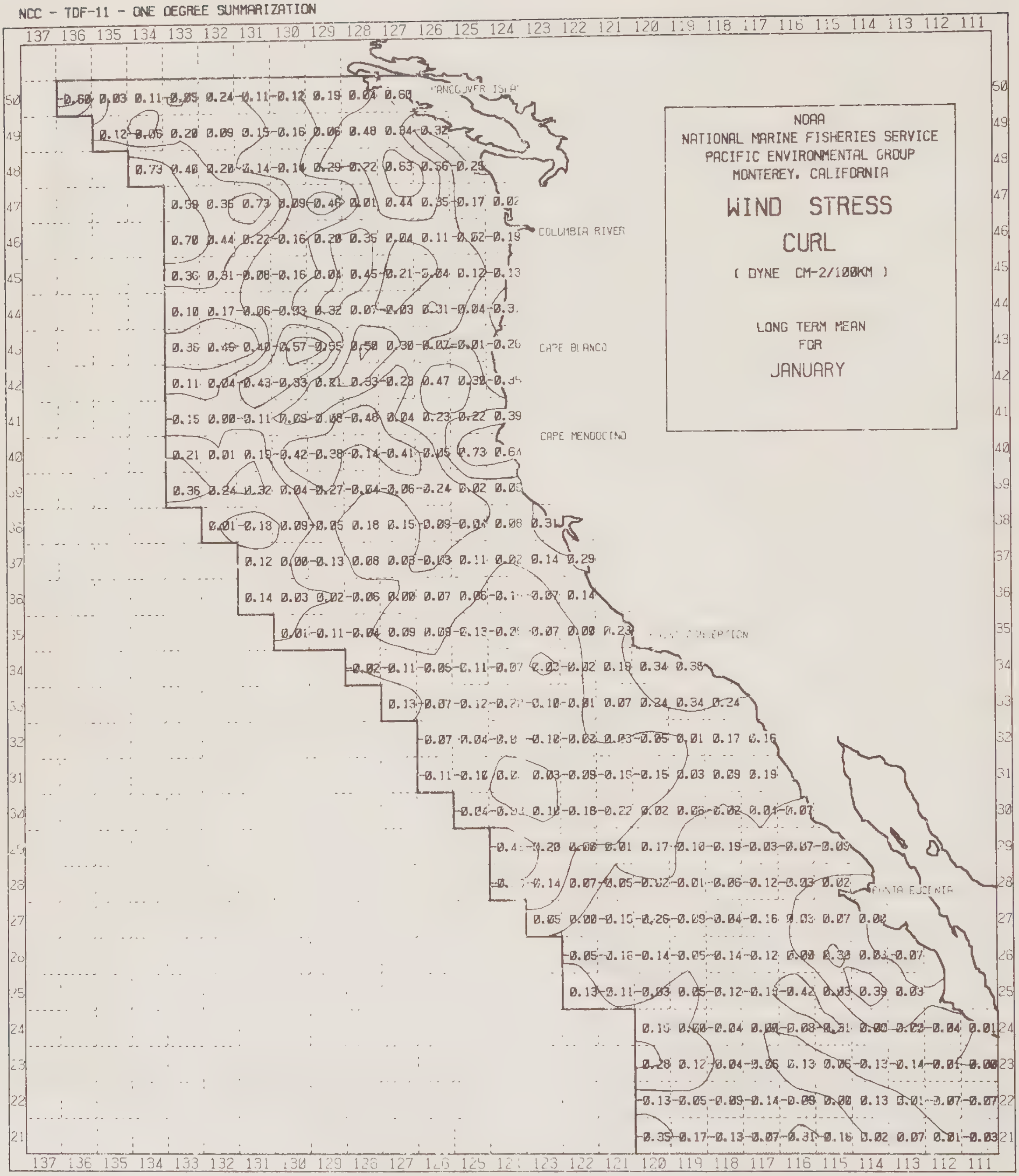
LAT/LON	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
48 N 125 W	.06 .05 930	.06 .06 739	.04 .06 848	.03 .04 770	.02 .02 767	.01 .01 763	.01 .01 1213	.01 .02 1138	.02 .03 754	.03 .05 795	.05 .05 823	.07 .08 629
48 N 126 W	.12 .12 304	.11 .09 209	.10 .08 252	.07 .07 198	.06 .09 185	.05 .05 197	.02 .03 324	.02 .02 327	.03 .04 298	.07 .05 400	.09 .09 331	.12 .12 201
48 N 127 W	.12 .12 143	.12 .13 131	.10 .12 130	.09 .14 101	.08 .10 151	.06 .07 140	.06 .07 137	.04 .06 134	.04 .06 206	.09 .11 136	.09 .11 247	.17 .15 137
48 N 128 W	.12 .14 114	.11 .16 131	.09 .09 139	.06 .08 147	.06 .08 148	.05 .06 133	.05 .08 118	.05 .07 115	.08 .14 130	.13 .14 134	.14 .16 142	.15 .16 136
48 N 129 W	.12 .17 111	.14 .12 125	.10 .11 126	.07 .10 110	.06 .08 147	.05 .08 113	.05 .08 135	.04 .08 131	.08 .14 141	.11 .15 117	.13 .16 114	.13 .15 122
48 N 130 W	.14 .15 132	.11 .17 108	.09 .10 136	.13 .11 123	.07 .09 131	.45 .18 138	.06 .09 120	.04 .06 148	.08 .09 179	.10 .15 131	.14 .16 134	.15 .16 141
48 N 131 W	.19 .18 143	.11 .13 126	.11 .12 134	.05 .07 167	.05 .06 207	.04 .05 168	.03 .04 173	.04 .06 161	.07 .09 178	.10 .14 169	.11 .16 162	.10 .15 184
48 N 132 W	.08 .08 322	.07 .07 302	.06 .06 335	.05 .07 321	.03 .04 380	.03 .05 205	.04 .06 192	.04 .05 192	.07 .08 209	.13 .13 161	.11 .12 197	.08 .10 295
48 N 133 W	.12 .13 124	.14 .16 95	.13 .15 116	.08 .12 134	.08 .08 136	.07 .07 133	.04 .05 137	.06 .09 107	.10 .09 147	.13 .12 143	.12 .16 147	.15 .15 153
48 N 134 W	.16 .17 82	.18 .26 107	.15 .14 97	.13 .13 104	.08 .07 118	.06 .08 118	.05 .05 94	.08 .07 91	.10 .13 96	.22 .34 114	.13 .14 132	.28 .25 114
49 N 126 W	.20 .13 98	.09 .09 140	.20 .13 124	.08 .08 141	.06 .05 149	.06 .05 145	.03 .02 406	.02 .02 378	.05 .04 235	.07 .06 207	.09 .12 122	.15 .16 106
49 N 127 W	.12 .12 152	.09 .10 159	.10 .12 170	.08 .10 193	.06 .06 213	.05 .06 209	.04 .03 331	.03 .03 283	.06 .06 268	.08 .08 223	.26 .16 212	.12 .11 169
49 N 128 W	.13 .13 185	.08 .12 175	.10 .09 234	.06 .09 197	.04 .05 453	.04 .05 273	.04 .05 325	.04 .04 322	.06 .07 272	.10 .11 207	.10 .10 267	.14 .13 184
49 N 129 W	.11 .14 184	.10 .09 190	.09 .09 212	.05 .09 245	.05 .06 289	.04 .05 241	.04 .05 272	.03 .05 251	.05 .08 249	.09 .11 233	.09 .11 246	.13 .14 194
49 N 130 W	.13 .12 308	.09 .11 316	.06 .07 314	.06 .07 316	.04 .05 298	.03 .04 298	.03 .05 303	.03 .05 325	.05 .06 345	.07 .09 280	.07 .08 332	.11 .12 304
49 N 131 W	.09 .09 430	.09 .09 388	.06 .08 411	.05 .08 452	.04 .05 330	.02 .03 520	.04 .05 458	.03 .04 330	.05 .06 420	.05 .06 362	.07 .08 368	.07 .11 406
49 N 132 W	.15 .14 182	.10 .11 197	.10 .11 189	.09 .09 191	.05 .05 240	.06 .06 211	.03 .04 235	.04 .05 220	.06 .08 225	.09 .10 227	.11 .10 235	.12 .11 217
49 N 133 W	.11 .14 196	.10 .12 185	.11 .08 225	.07 .09 250	.06 .06 235	.04 .05 244	.03 .04 220	.04 .05 272	.06 .07 251	.11 .10 233	.13 .13 238	.11 .13 190
49 N 134 W	.14 .13 200	.12 .11 179	.10 .09 201	.09 .12 210	.05 .06 249	.05 .05 240	.04 .04 227	.04 .05 252	.07 .07 277	.11 .12 257	.11 .12 262	.11 .12 211
49 N 135 W	.12 .11 183	.11 .11 165	.10 .11 199	.09 .12 217	.08 .07 213	.08 .05 200	.05 .05 184	.05 .06 211	.06 .07 263	.08 .11 243	.09 .11 306	.11 .10 241
50 N 127 W	.38 .26 19	.17 .16 30	.28 .33 20	.55 .32 35	.09 .02 59	.09 .10 27	.05 .05 86	.04 .01 88	.03 .02 160	.10 .07 112	2.75 .51 53	.54 .55 17
50 N 128 W	.18 .17 68	.33 .35 48	.19 .13 68	.11 .17 69	.13 .13 62	.08 .10 95	.09 .08 102	.06 .09 69	.09 .12 77	.10 .10 81	.12 .17 84	.32 .27 61
50 N 129 W	.17 .20 93	.18 .16 78	.13 .17 89	.11 .15 110	.06 .07 136	.08 .09 116	.05 .06 171	.05 .07 148	.07 .11 129	.13 .14 98	.20 .18 106	.22 .24 82
50 N 130 W	.19 .14 124	.13 .13 113	.15 .14 121	.07 .10 140	.05 .06 189	.06 .06 210	.04 .07 216	.05 .07 183	.05 .09 187	.11 .11 152	.13 .20 139	.11 .13 110
50 N 131 W	.13 .17 163	.12 .13 149	.10 .11 160	.07 .10 217	.05 .06 253	.05 .06 202	.04 .05 273	.04 .05 240	.07 .09 248	.10 .10 180	.11 .12 187	.12 .15 154
50 N 132 W	.12 .16 138	.12 .13 129	.12 .10 160	.08 .08 173	.05 .06 223	.04 .06 213	.04 .05 254	.09 .23 234	.06 .08 228	.12 .16 148	.13 .12 170	.14 .23 125
50 N 133 W	.14 .16 125	.14 .14 129	.15 .13 137	.06 .08 189	.06 .06 212	.06 .07 185	.04 .05 214	.04 .05 230	.07 .08 203	.14 .12 166	.16 .15 147	.16 .17 144
50 N 134 W	.12 .11 327	.08 .10 261	.07 .06 331	.06 .08 309	.04 .05 328	.03 .04 409	.03 .04 335	.04 .04 313	.07 .08 203	.11 .11 163	.11 .10 284	.10 .12 289
50 N 135 W	.14 .15 161	.13 .11 162	.11 .11 197	.08 .08 212	.05 .05 255	.04 .04 263	.03 .04 237	.05 .06 237	.05 .06 484	.10 .11 228	.11 .13 222	.15 .15 188
50 N 136 W	.08 .08 485	.09 .08 463	.05 .05 649	.04 .05 681	.04 .04 595	.04 .04 537	.03 .03 384	.04 .04 406	.04 .06 446	.07 .08 499	.08 .07 536	.09 .09 566

APPENDIX III

Monthly Wind Stress Curl Distributions

The monthly mean wind stress curl distributions are displayed in Charts 37 to 48. The plotted values are estimates of the vertical component of the wind stress curl, calculated by applying a finite difference, spherical coordinate curl operator to the fields of monthly mean surface wind stress. The contoured values are plotted in units of dyne cm^{-2} per 100 km. A value of 1.0 dyne cm^{-2} per 100 km is equivalent to 1.0×10^{-7} dyne cm^{-3}. The contour interval is 0.25 dyne cm^{-2} per 100 km. Positive wind stress curl is associated with surface Ekman divergence (upwelling). Negative values are shaded. These correspond to surface Ekman convergence (downwelling).

In the following charts, the month is indicated in the figure legend in the upper right corner of the charts. The coastline configuration is superimposed on the grid as a visual aid and does not represent a conformal mapping.



NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
WIND STRESS
CURL
(DYNE CM-2/100KM)
LONG TERM MEAN
FOR
JANUARY
VANCOUVER ISLA
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
PT. CONCEPTION
PUNTA EUGENIA
-0.60 0.03 0.11 -0.05 0.24 -0.11 -0.12 0.19 0.04 0.60
0.12 -0.06 0.20 0.09 0.15 -0.16 0.06 0.48 0.34 -0.32
0.73 0.40 0.20 -0.14 -0.14 0.29 -0.22 0.63 0.56 -0.29
0.59 0.36 0.73 0.09 -0.46 0.01 0.44 0.35 -0.17 0.02
0.70 0.44 0.22 -0.16 0.20 0.35 0.04 0.11 -0.02 -0.19
0.30 0.31 -0.08 -0.16 0.04 0.45 -0.21 -0.04 0.12 -0.13
0.10 0.17 -0.06 -0.33 0.32 0.07 -0.03 0.31 -0.04 -0.3
0.36 0.49 0.40 -0.57 -0.55 0.50 0.30 -0.07 -0.01 -0.20
0.11 0.04 -0.43 -0.33 0.21 0.33 -0.23 0.47 0.30 -0.34
-0.15 0.00 -0.11 -0.09 -0.08 -0.46 0.04 0.23 0.22 0.39
0.21 0.01 0.19 -0.42 -0.38 -0.14 -0.41 -0.05 0.73 0.64
0.36 0.24 0.32 0.04 -0.27 -0.04 -0.06 -0.24 0.02 0.05
0.01 -0.18 0.09 -0.05 0.18 0.15 -0.09 -0.04 0.08 0.31
0.12 0.00 -0.13 0.08 0.03 -0.03 0.11 0.02 0.14 0.29
0.14 0.03 0.02 -0.06 0.00 0.07 0.06 -0.1 -0.07 0.14
0.01 -0.11 -0.04 0.09 0.09 -0.13 -0.29 -0.07 0.00 0.23
-0.02 -0.11 -0.05 -0.11 -0.07 0.02 -0.02 0.19 0.34 0.38
0.13 -0.07 -0.12 -0.27 -0.10 -0.01 0.07 0.24 0.34 0.24
-0.07 -0.04 -0.0 -0.10 -0.02 0.03 -0.05 0.01 0.17 0.16
-0.11 -0.10 0.0 0.03 -0.09 -0.19 -0.15 0.03 0.09 0.19
-0.04 -0.3 0.10 -0.18 -0.22 0.02 0.06 -0.02 0.04 -0.07
-0.4 -0.20 0.08 0.01 0.17 -0.10 -0.19 -0.03 -0.07 -0.09
-0. -0.14 0.07 -0.05 -0.02 -0.01 -0.06 -0.12 -0.03 0.02
0.05 0.00 -0.15 -0.26 -0.09 -0.04 -0.16 0.03 0.07 0.00
-0.05 -0.16 -0.14 -0.05 -0.14 -0.12 0.00 0.30 0.03 -0.07
0.13 -0.11 -0.03 0.05 -0.12 -0.13 -0.42 0.03 0.39 0.03
0.15 0.00 -0.04 0.00 -0.08 -0.31 0.00 -0.02 -0.04 0.01
0.28 0.12 -0.04 -0.06 0.13 0.06 -0.13 -0.14 -0.01 -0.00
-0.13 -0.05 -0.09 -0.14 -0.09 0.00 0.13 0.01 -0.07 -0.07
-0.35 -0.17 -0.13 -0.07 -0.31 -0.16 0.02 0.07 0.01 -0.03

Chart 37.—Wind stress curl for January.

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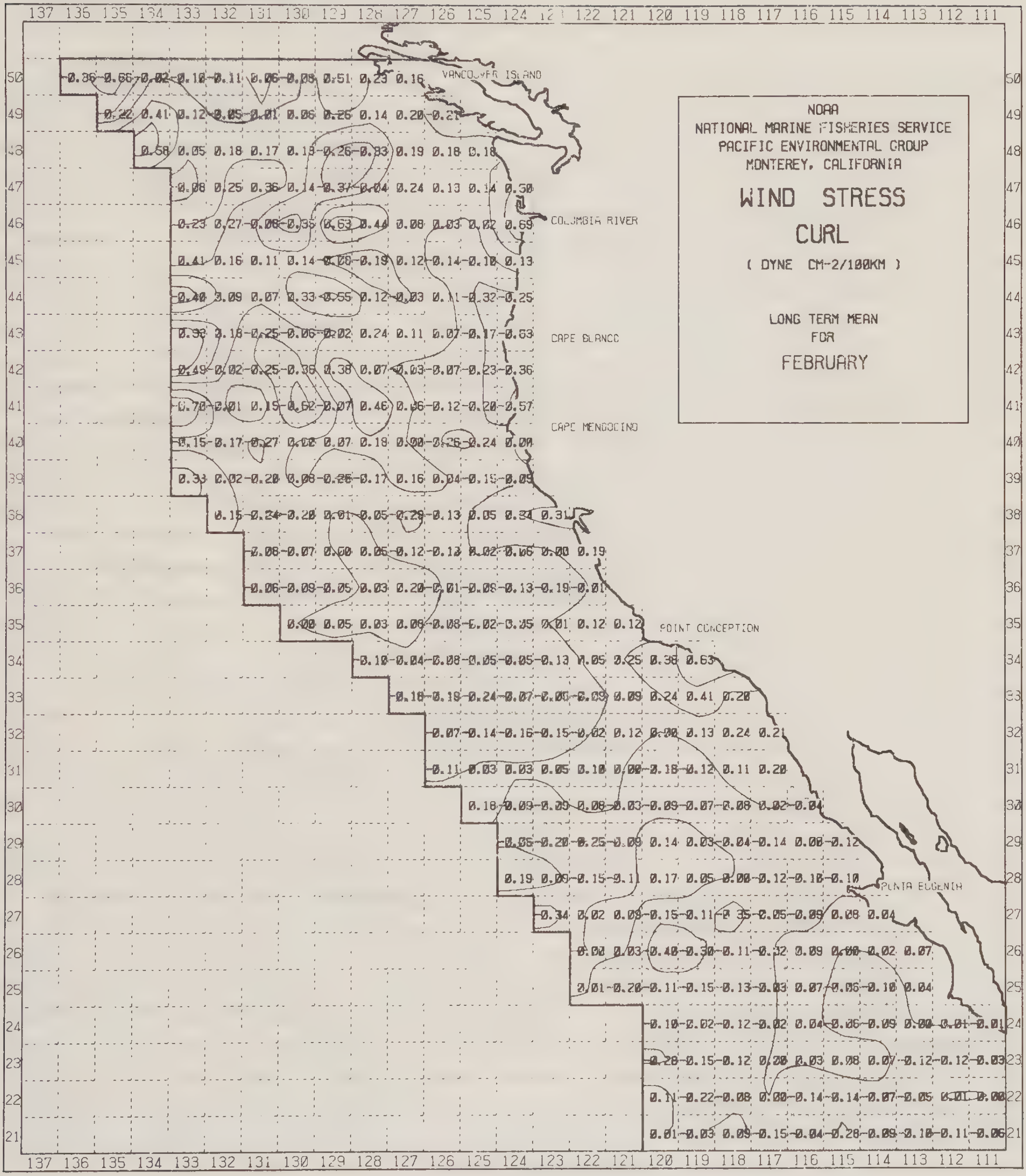
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
WIND STRESS
CURL
(DYNE CM-2/100KM)
LONG TERM MEAN
FOR
FEBRUARY
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
-0.36-0.66-0.02-0.10-0.11 0.06-0.08 0.51 0.23 0.16
0.22 0.41 0.12-0.05-0.01 0.06 0.26 0.14 0.20-0.21
0.58 0.05 0.18 0.17 0.13-0.26-0.33 0.19 0.18 0.18
-0.08 0.25 0.36 0.14-0.37-0.04 0.24 0.13 0.14 0.50
-0.23 0.27-0.08-0.35 0.63 0.44 0.08 0.03 0.02 0.69
0.41 0.16 0.11 0.14-0.20-0.19 0.12-0.14-0.10 0.13
-0.40 0.09 0.07 0.33-0.55 0.12-0.03 0.11-0.32-0.25
0.32 0.16-0.25-0.06-0.02 0.24 0.11 0.07-0.17-0.63
0.49-0.02-0.25-0.36 0.38 0.07-0.03-0.07-0.23-0.36
-0.70-0.01 0.15-0.62-0.07 0.46 0.06-0.12-0.20-0.57
-0.15-0.17-0.27 0.02 0.07 0.18 0.00-0.26-0.24 0.00
0.33 0.02-0.20 0.08-0.26-0.17 0.16 0.04-0.15-0.09
0.15-0.24-0.20 0.01-0.05-0.29-0.13 0.05 0.34 0.31
-0.08-0.07 0.60 0.05-0.12-0.13 0.02-0.06 0.00 0.19
-0.06-0.09-0.05 0.03 0.20-0.01-0.09-0.13-0.19-0.01
0.00 0.05 0.03 0.06-0.08-0.02-0.05 0.01 0.12 0.12
-0.10-0.04-0.08-0.05-0.05-0.13 0.05 0.25 0.36 0.63
-0.16-0.19-0.24-0.07-0.05-0.09 0.09 0.24 0.41 0.20
-0.07-0.14-0.16-0.15-0.02 0.12 0.00 0.13 0.24 0.21
-0.11 0.03 0.03 0.05 0.10 0.00-0.18-0.12 0.11 0.20
0.16-0.09-0.25 0.08-0.03-0.09-0.07-0.08 0.02-0.04
-0.06-0.20-0.25-0.09 0.14 0.03-0.04-0.14 0.00-0.12
0.19 0.09-0.15-0.11 0.17 0.05 0.00-0.12-0.16-0.10
-0.34 0.02 0.09-0.15-0.11-0.35-0.05-0.09 0.08 0.04
0.00 0.03-0.40-0.30-0.11-0.32 0.09 0.00 0.02 0.07
0.01-0.20-0.11-0.15-0.13-0.03 0.07-0.06-0.10 0.04
-0.10-0.02-0.12-0.02 0.04-0.06-0.09 0.00 0.01-0.01
-0.20-0.15-0.12 0.20 0.03 0.08 0.07-0.12-0.12-0.03
0.11-0.22-0.08 0.00-0.14-0.14-0.07-0.05 0.01 0.00
0.01-0.03 0.09-0.15-0.04-0.28-0.09-0.10-0.11-0.06

Chart 38.—Wind stress curl for February.

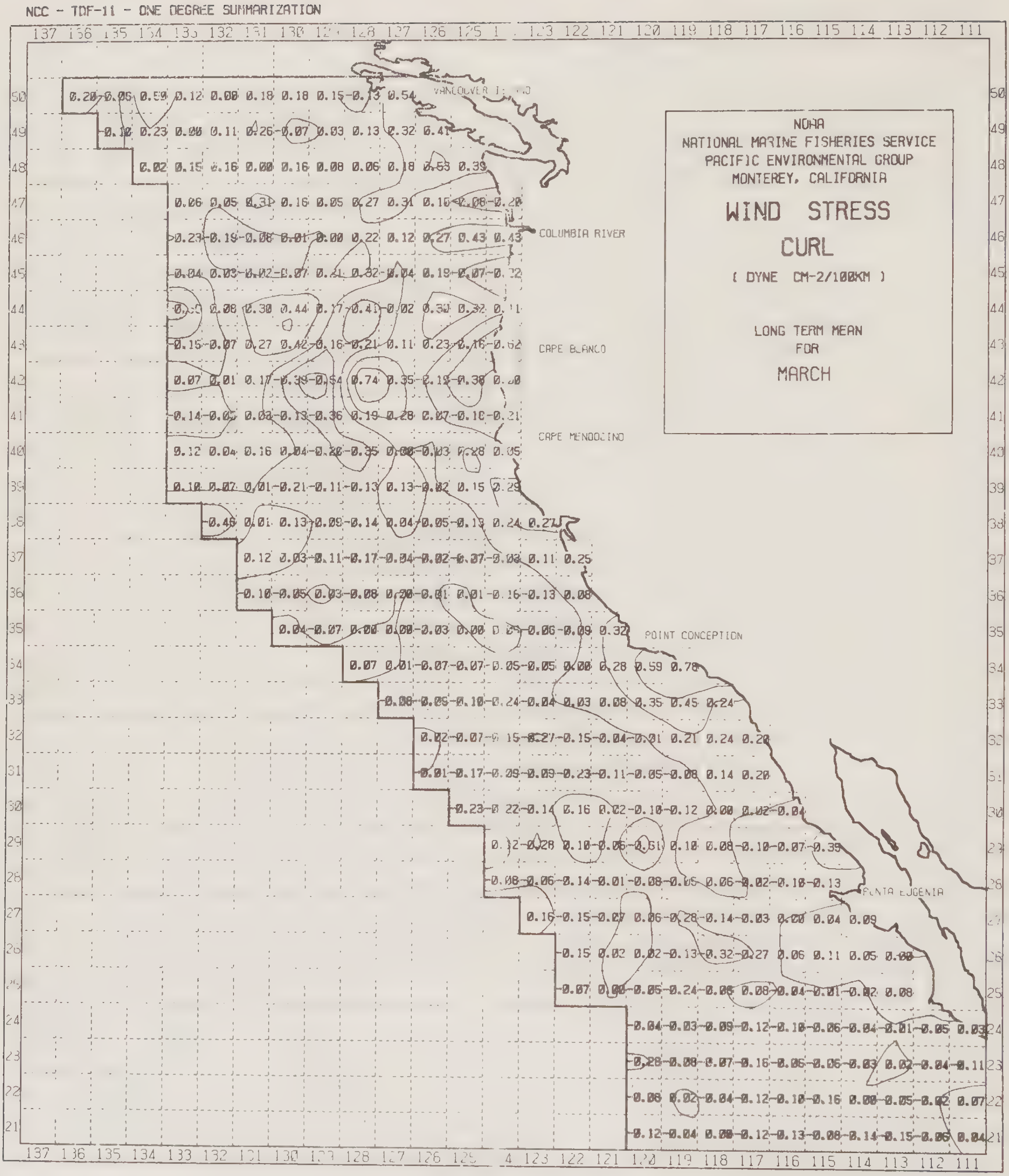
NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
WIND STRESS
CURL
(DYNE CM-2/100KM)
LONG TERM MEAN
FOR
MARCH
VANCOUVER I.
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
0.20 -0.06 0.59 0.12 0.00 0.18 0.18 0.15 -0.13 0.54
-0.10 0.23 0.00 0.11 0.26 -0.07 0.03 0.13 0.32 0.41
0.02 0.15 0.16 0.00 0.16 0.08 0.06 0.18 0.53 0.39
0.06 0.05 0.31 0.16 0.05 0.27 0.31 0.10 -0.08 -0.20
-0.23 -0.19 -0.06 0.01 0.00 0.22 0.12 0.27 0.43 0.43
-0.04 0.03 -0.02 -0.07 0.21 0.32 -0.04 0.19 -0.07 -0.22
0.08 0.30 0.44 0.17 -0.41 -0.02 0.30 0.32 0.11
-0.15 -0.07 0.27 0.42 -0.16 -0.21 0.11 0.23 -0.16 -0.62
0.07 0.01 0.17 -0.39 -0.54 0.74 0.35 -0.19 -0.38
-0.14 -0.05 0.03 -0.13 -0.36 0.19 -0.28 0.07 -0.10 -0.21
0.12 0.04 0.16 0.04 -0.20 -0.35 0.00 -0.03 0.28 0.05
0.10 0.07 0.01 -0.21 -0.11 -0.13 0.13 -0.02 0.15 0.29
-0.46 0.01 0.13 -0.09 -0.14 0.04 -0.05 -0.13 0.24 0.27
0.12 0.03 -0.11 -0.17 -0.04 -0.02 -0.07 -0.03 0.11 0.25
-0.10 -0.05 0.03 -0.08 0.20 -0.01 0.01 -0.16 -0.13 0.08
0.04 -0.07 0.00 0.00 -0.03 0.00 0.29 -0.06 -0.09 0.32
0.07 0.01 -0.07 -0.07 -0.05 -0.05 0.00 0.28 0.59 0.78
-0.08 -0.09 -0.10 -0.24 -0.04 0.03 0.08 0.35 0.45 0.24
0.02 -0.07 -0.15 -0.27 -0.15 -0.04 -0.01 0.21 0.24 0.20
-0.01 -0.17 -0.09 -0.09 -0.23 -0.11 -0.05 -0.08 0.14 0.20
-0.23 -0.22 -0.14 0.16 0.02 -0.10 -0.12 0.00 0.02 -0.04
0.12 -0.28 0.10 -0.06 -0.51 0.10 0.08 -0.10 -0.07 -0.39
-0.08 -0.06 -0.14 -0.01 -0.08 -0.05 0.06 -0.02 -0.10 -0.13
0.16 -0.15 -0.27 0.06 -0.28 -0.14 -0.03 0.00 0.04 0.09
-0.15 0.02 0.02 -0.13 -0.32 -0.27 0.06 0.11 0.05 0.00
-0.07 0.00 -0.05 -0.24 -0.06 0.08 -0.04 -0.01 -0.02 0.08
-0.04 -0.03 -0.09 -0.12 -0.10 -0.06 -0.04 -0.01 -0.05 0.03
-0.28 -0.08 -0.07 -0.16 -0.06 -0.06 -0.03 0.02 -0.04 -0.11
-0.08 0.02 -0.04 -0.12 -0.10 -0.16 0.00 -0.05 -0.02 0.07
-0.12 -0.04 0.00 -0.12 -0.13 -0.08 -0.14 -0.15 -0.06 0.04

Chart 39.—Wind stress curl for March.

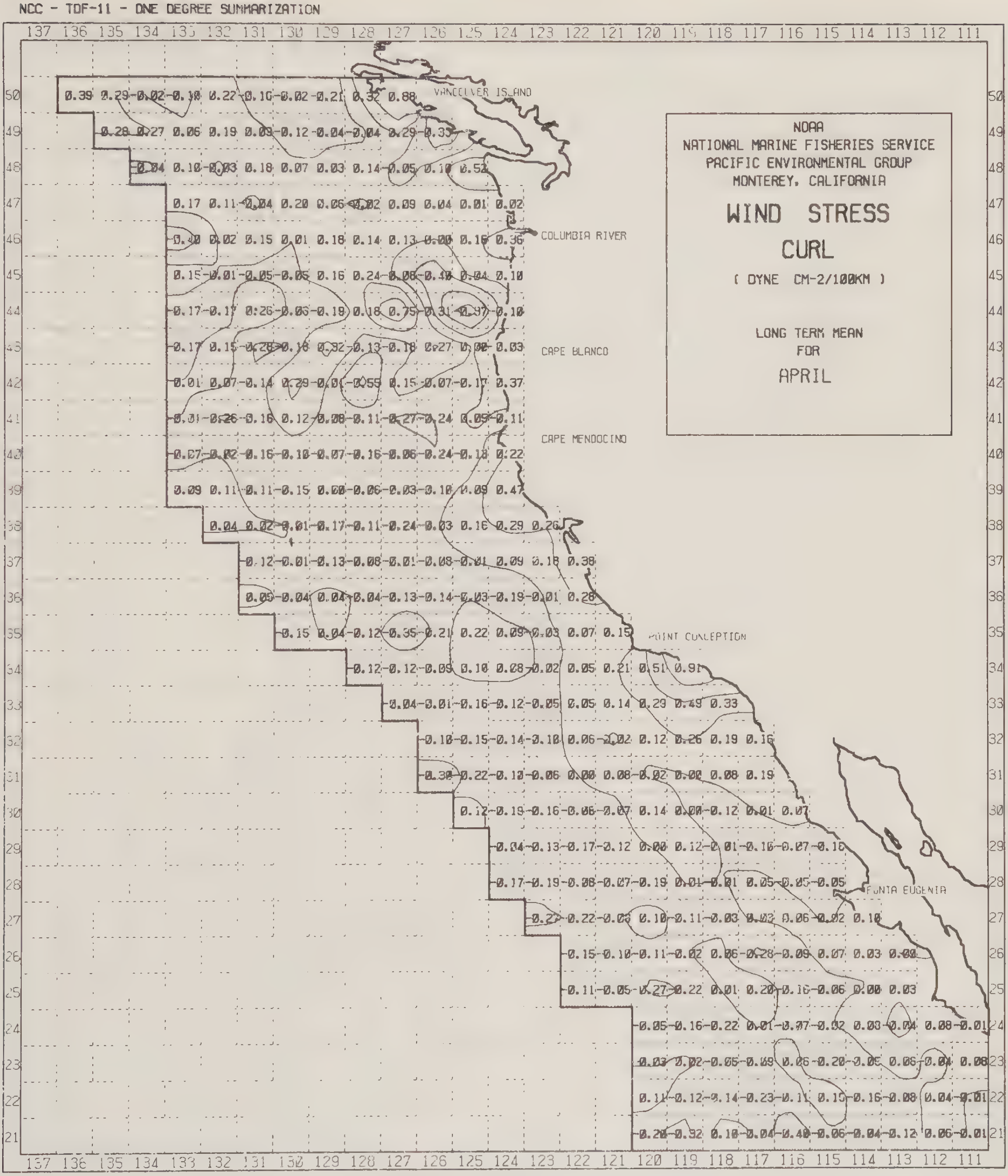
NCC - TDF-11 - ONE DEGREE SUMMARIZATION
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
WIND STRESS
CURL
(DYNE CM-2/100KM)
LONG TERM MEAN
FOR
APRIL
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21

Chart 40.—Wind stress curl for April.

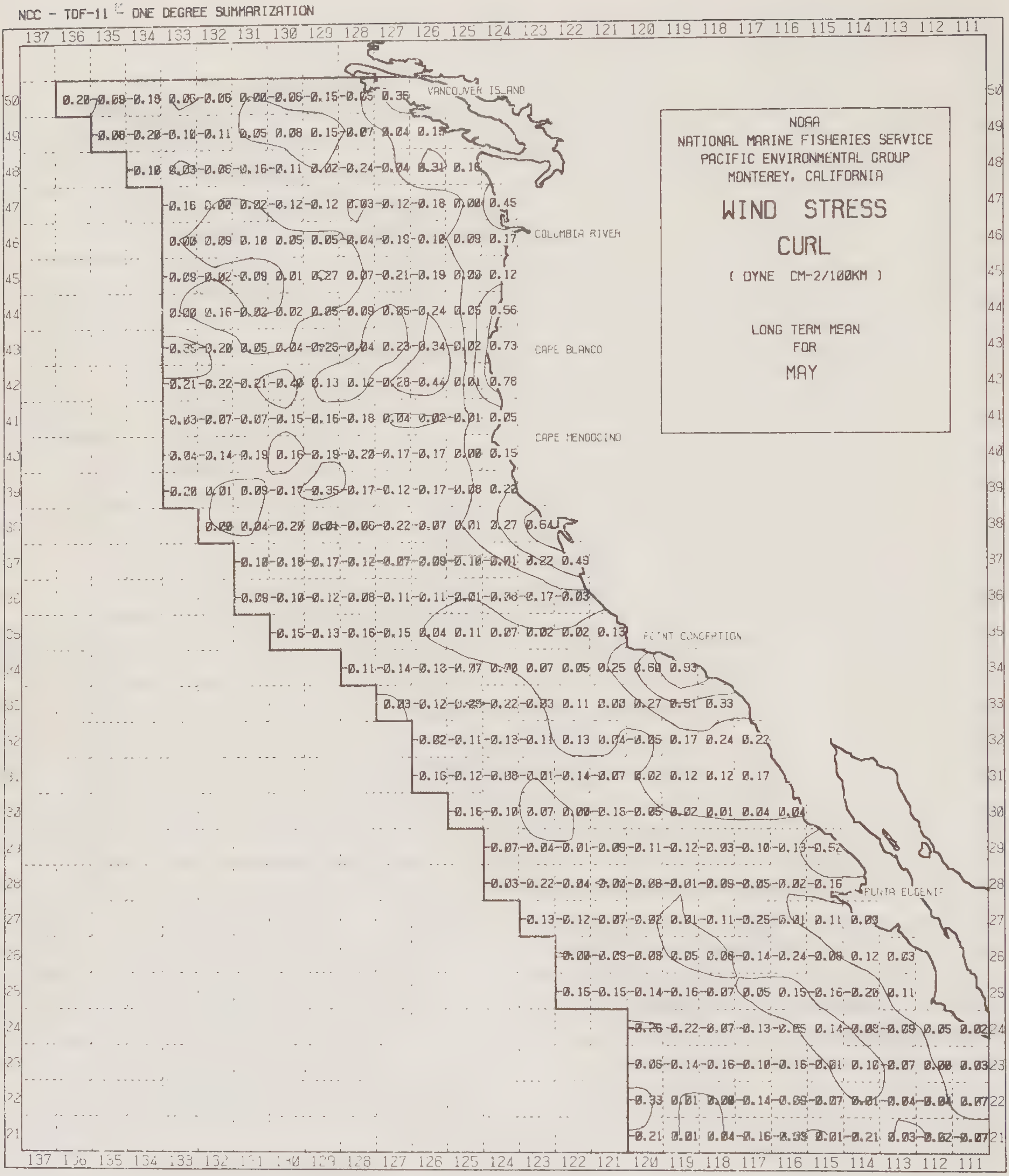
NCC - TDF-11 ONE DEGREE SUMMARIZATION
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
WIND STRESS
CURL
(DYNE CM-2/100KM)
LONG TERM MEAN
FOR
MAY
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21

Chart 41.—Wind stress curl for May.

NCC - TDF-11 - ONE DEGREE SUMMARIZATION

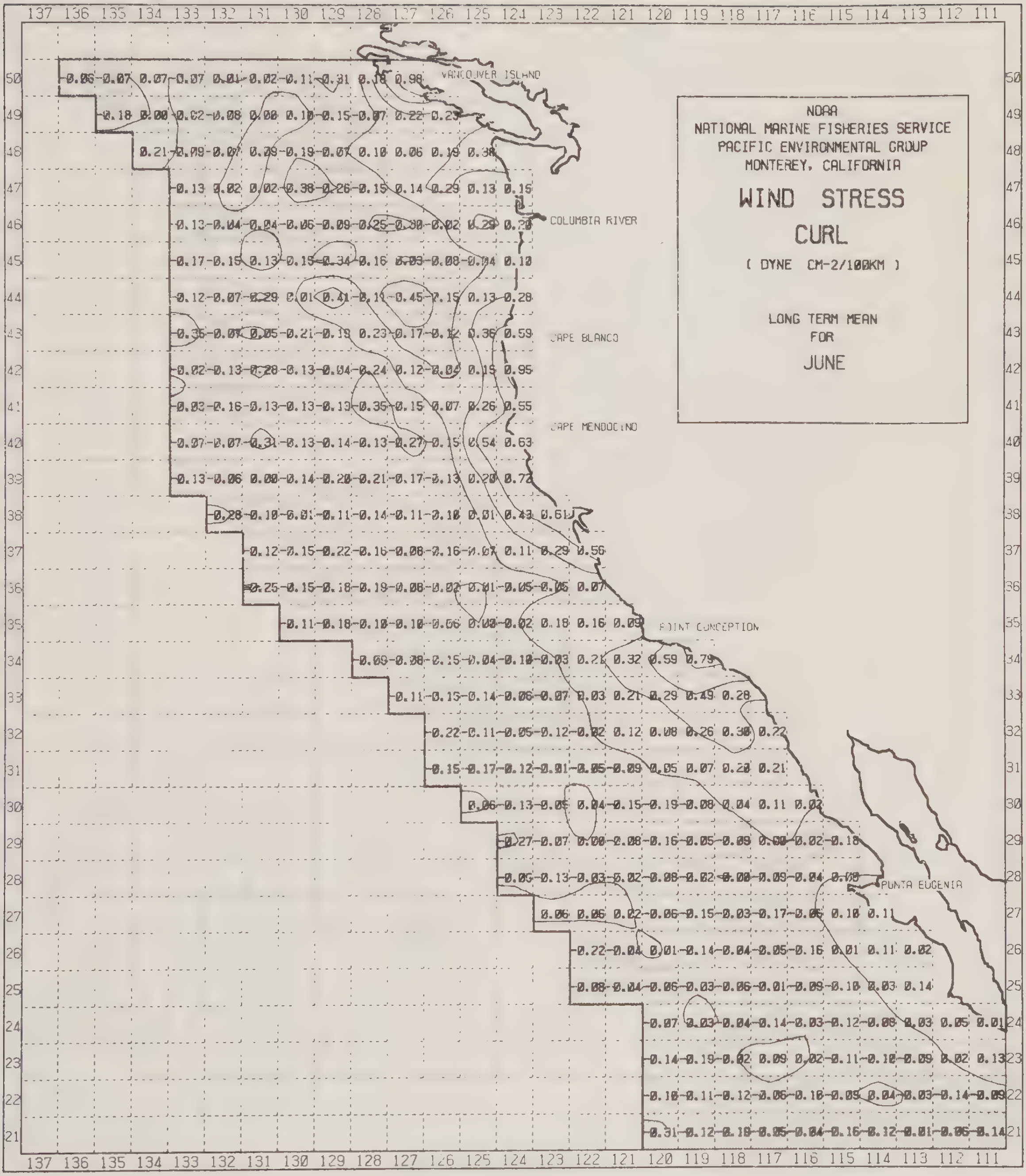
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
WIND STRESS
CURL
(DYNE CM-2/100KM)
LONG TERM MEAN
FOR
JUNE
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 -0.06 -0.07 0.07 -0.07 0.01 -0.02 -0.11 -0.31 0.18 0.98
49 -0.18 0.00 -0.02 -0.08 0.00 0.10 -0.15 -0.07 0.22 0.23
48 0.21 -0.09 -0.07 0.29 -0.19 -0.07 0.10 0.06 0.19 0.38
47 -0.13 0.02 0.02 -0.38 -0.26 -0.15 0.14 0.29 0.13 0.15
46 -0.13 -0.04 -0.04 -0.06 -0.09 -0.25 -0.30 -0.02 0.29 0.70
45 -0.17 -0.15 0.13 -0.15 -0.34 -0.16 0.03 -0.08 -0.04 0.10
44 -0.12 -0.07 -0.29 0.01 0.41 -0.11 -0.45 -0.15 0.13 -0.28
43 -0.35 -0.07 0.05 -0.21 -0.19 0.23 -0.17 -0.12 0.36 0.59
42 -0.02 -0.13 -0.28 -0.13 -0.04 -0.24 0.12 -0.04 0.15 0.95
41 -0.03 -0.16 -0.13 -0.13 -0.13 -0.35 -0.15 0.07 0.26 0.55
40 -0.07 -0.07 -0.31 -0.13 -0.14 -0.13 -0.27 -0.15 0.54 0.63
39 -0.13 -0.06 0.00 -0.14 -0.20 -0.21 -0.17 -0.13 0.20 0.72
38 -0.28 -0.10 -0.01 -0.11 -0.14 -0.11 -0.10 0.01 0.43 0.61
37 -0.12 -0.15 -0.22 -0.16 -0.08 -0.16 -0.07 0.11 0.29 0.56
36 -0.25 -0.15 -0.18 -0.19 -0.08 -0.02 0.01 -0.05 -0.05 0.07
35 -0.11 -0.18 -0.10 -0.10 -0.06 0.00 -0.02 0.18 0.16 0.09
34 -0.09 -0.08 -0.15 -0.04 -0.10 -0.03 0.21 0.32 0.59 0.79
33 -0.11 -0.15 -0.14 -0.06 -0.07 0.03 0.21 0.29 0.49 0.28
32 -0.22 -0.11 -0.05 -0.12 -0.02 0.12 0.08 0.26 0.30 0.22
31 -0.15 -0.17 -0.12 -0.01 -0.05 -0.09 0.05 0.07 0.20 0.21
30 0.06 -0.13 -0.05 0.04 -0.15 -0.19 -0.08 0.04 0.11 0.02
29 -0.27 -0.07 0.00 -0.08 -0.16 -0.05 -0.09 0.00 -0.02 -0.18
28 -0.05 -0.13 -0.03 -0.02 -0.08 -0.02 -0.00 -0.09 -0.04 0.00
27 0.06 0.06 0.02 -0.06 -0.15 -0.03 -0.17 -0.06 0.10 0.11
26 -0.22 -0.04 0.01 -0.14 -0.04 -0.05 -0.16 0.01 0.11 0.02
25 -0.08 -0.04 -0.06 -0.03 -0.06 -0.01 -0.09 -0.10 0.03 0.14
24 -0.07 0.03 -0.04 -0.14 -0.03 -0.12 -0.08 0.03 0.05 0.01
23 -0.14 -0.19 -0.02 0.09 0.02 -0.11 -0.10 -0.09 0.02 0.13
22 -0.10 -0.11 -0.12 -0.06 -0.10 -0.05 0.04 -0.03 -0.14 -0.09
21 -0.31 -0.12 -0.19 -0.05 -0.04 -0.16 -0.12 -0.01 -0.06 -0.14

Chart 42.—Wind stress curl for June.

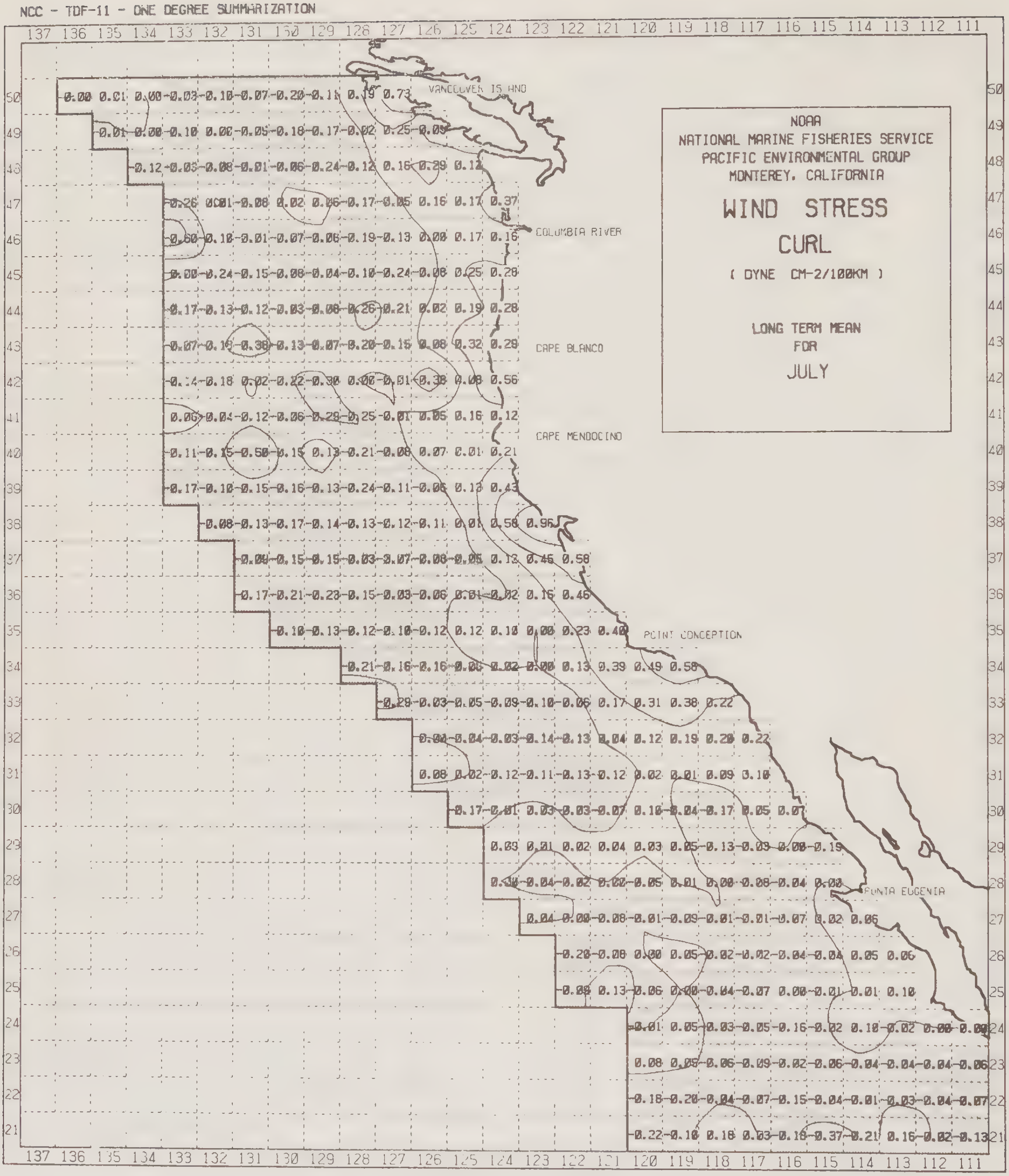
NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
WIND STRESS
CURL
(DYNE CM-2/100KM)
LONG TERM MEAN
FOR
JULY
VANCOUVER IS AND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
-0.00 0.01 0.00 -0.03 -0.10 -0.07 -0.20 -0.11 0.19 0.73
-0.01 0.00 -0.10 0.02 -0.05 -0.18 -0.17 -0.02 0.25 -0.09
-0.12 -0.05 -0.08 -0.01 -0.06 -0.24 -0.12 0.16 0.29 0.12
-0.26 0.01 -0.08 0.02 0.06 -0.17 -0.05 0.16 0.17 0.37
-0.50 -0.10 -0.01 -0.07 -0.06 -0.19 -0.13 0.00 0.17 0.16
-0.00 -0.24 -0.15 -0.08 -0.04 -0.10 -0.24 -0.08 0.25 0.28
-0.17 -0.13 -0.12 -0.03 -0.08 -0.26 -0.21 0.02 0.19 0.28
-0.07 -0.16 -0.38 -0.13 -0.07 -0.20 -0.15 0.08 0.32 0.29
-0.14 -0.18 0.02 -0.22 -0.30 0.00 -0.01 -0.38 0.08 0.56
0.06 -0.04 -0.12 -0.06 -0.28 -0.25 -0.01 0.05 0.16 0.12
-0.11 -0.15 -0.50 -0.15 0.13 -0.21 -0.08 0.07 0.01 0.21
-0.17 -0.10 -0.15 -0.16 -0.13 -0.24 -0.11 -0.06 0.13 0.43
-0.08 -0.13 -0.17 -0.14 -0.13 -0.12 -0.11 0.01 0.58 0.96
-0.09 -0.15 -0.15 -0.03 -0.07 -0.08 -0.05 0.12 0.45 0.58
-0.17 -0.21 -0.23 -0.15 -0.03 -0.06 0.01 -0.02 0.16 0.45
-0.10 -0.13 -0.12 -0.10 -0.12 0.12 0.10 0.00 0.23 0.40
-0.21 -0.16 -0.16 -0.06 0.02 0.00 0.13 0.39 0.49 0.58
-0.29 -0.03 -0.05 -0.09 -0.10 -0.06 0.17 0.31 0.38 0.22
-0.00 -0.04 -0.03 -0.14 -0.13 0.04 0.12 0.19 0.20 0.22
0.08 0.02 -0.12 -0.11 -0.13 -0.12 0.02 0.01 0.09 0.10
-0.17 -0.01 0.03 -0.03 -0.07 0.10 -0.04 -0.17 0.05 0.07
0.09 0.01 0.02 0.04 0.03 0.05 -0.13 -0.03 -0.00 -0.15
0.30 -0.04 -0.02 0.02 -0.05 0.01 0.00 -0.08 -0.04 0.00
0.04 0.00 -0.08 -0.01 -0.09 -0.01 -0.01 -0.07 0.02 0.06
-0.20 -0.08 0.00 0.05 -0.02 -0.02 -0.04 -0.04 0.05 0.06
-0.09 0.13 -0.06 0.00 -0.04 -0.07 0.00 -0.01 -0.01 0.10
-0.01 0.05 -0.03 -0.05 -0.16 -0.02 0.10 -0.02 0.00 -0.00
0.08 0.05 -0.06 -0.09 -0.02 -0.06 -0.04 -0.04 -0.04 -0.06
-0.18 -0.20 -0.04 -0.07 -0.15 -0.04 -0.01 -0.03 -0.04 -0.07
-0.22 -0.10 0.18 0.03 -0.10 -0.37 -0.21 0.16 -0.02 -0.13

Chart 43.—Wind stress curl for July.

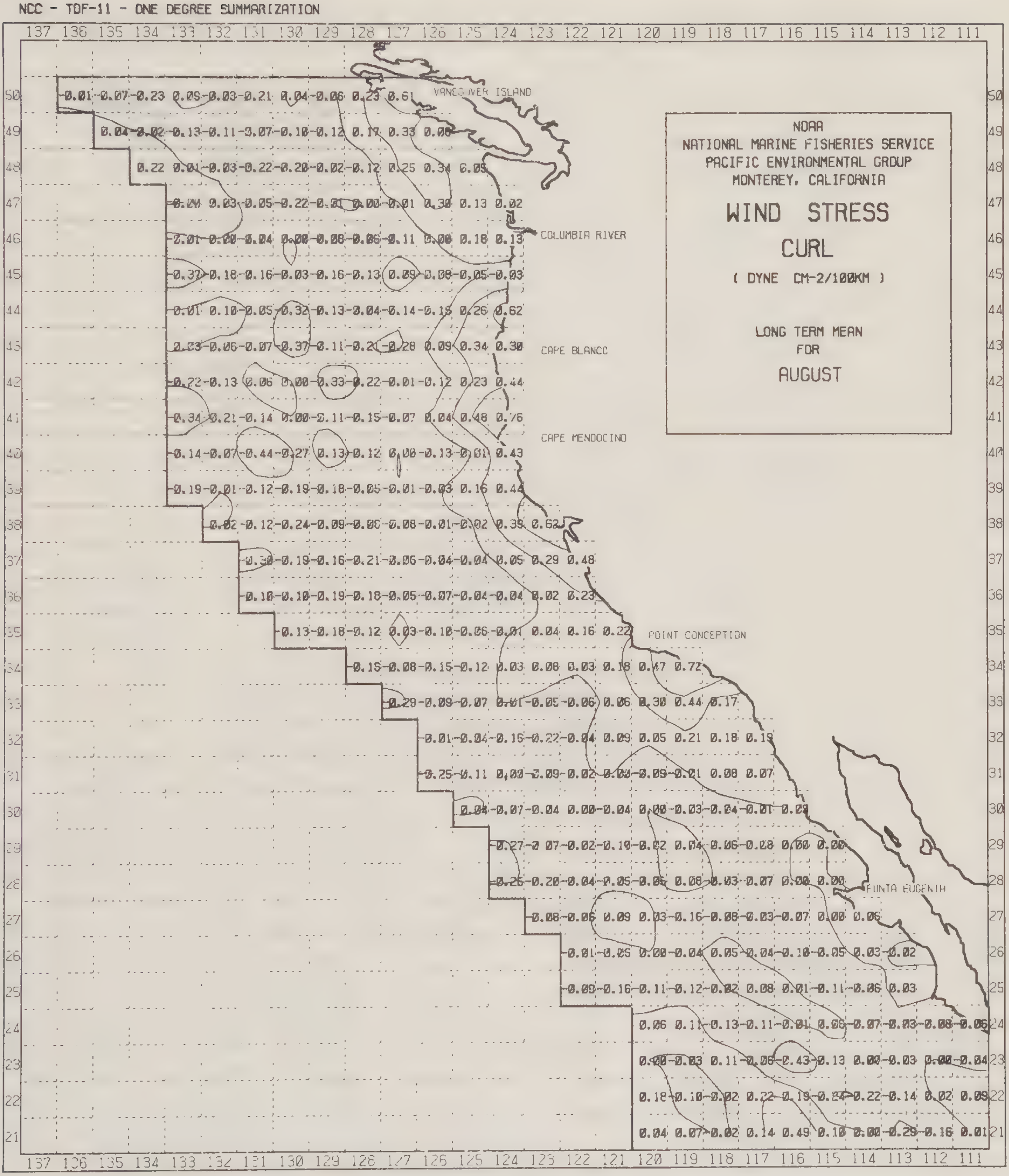
NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
WIND STRESS
CURL
(DYNE CM-2/100KM)
LONG TERM MEAN
FOR
AUGUST
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
50 -0.01 -0.07 -0.23 0.09 -0.03 -0.21 0.04 -0.06 0.23 0.61
49 0.04 -0.02 -0.13 -0.11 -0.07 -0.10 -0.12 0.17 0.33 0.08
48 0.22 0.01 -0.03 -0.22 -0.20 -0.02 -0.12 0.25 0.34 0.05
47 -0.04 0.03 -0.05 -0.22 -0.01 0.00 -0.01 0.30 0.13 0.02
46 -0.01 0.00 -0.04 0.00 -0.08 -0.06 -0.11 0.00 0.18 0.13
45 -0.37 -0.18 -0.16 -0.03 -0.16 -0.13 0.09 -0.08 -0.05 -0.03
44 -0.01 0.10 -0.05 -0.32 -0.13 -0.04 -0.14 -0.15 0.26 0.62
43 0.03 -0.06 -0.07 -0.37 -0.11 -0.21 -0.28 0.09 0.34 0.30
42 -0.22 -0.13 0.06 0.00 -0.33 -0.22 -0.01 -0.12 0.23 0.44
41 -0.34 -0.21 -0.14 0.00 -0.11 -0.15 -0.07 0.04 0.48 0.76
40 -0.14 -0.07 -0.44 -0.27 0.13 -0.12 0.00 -0.13 -0.01 0.43
39 -0.19 -0.01 -0.12 -0.19 -0.18 -0.05 -0.01 -0.03 0.16 0.44
38 0.02 -0.12 -0.24 -0.09 -0.06 -0.08 -0.01 -0.02 0.39 0.62
37 -0.30 -0.19 -0.16 -0.21 -0.06 -0.04 -0.04 0.05 0.29 0.48
36 -0.10 -0.10 -0.19 -0.18 -0.05 -0.07 -0.04 -0.04 0.02 0.23
35 -0.13 -0.18 -0.12 0.03 -0.10 -0.06 -0.01 0.04 0.16 0.22
34 -0.15 -0.08 -0.15 -0.12 0.03 0.08 0.03 0.18 0.47 0.72
33 -0.29 -0.09 -0.07 0.01 -0.05 -0.06 0.06 0.30 0.44 0.17
32 -0.01 -0.04 -0.16 -0.22 -0.04 0.09 0.05 0.21 0.18 0.19
31 -0.25 -0.11 0.00 -0.09 -0.02 0.00 -0.09 -0.01 0.08 0.07
30 0.04 -0.07 -0.04 0.00 -0.04 0.00 -0.03 -0.04 -0.01 0.03
29 -0.27 -0.07 -0.02 -0.10 -0.02 0.04 -0.06 -0.08 0.00 0.00
28 -0.25 -0.20 -0.04 -0.05 -0.05 0.08 -0.03 -0.07 0.00 0.00
27 -0.08 -0.06 0.09 0.03 -0.16 -0.08 -0.03 -0.07 0.00 0.06
26 -0.01 -0.05 0.00 -0.04 0.05 -0.04 -0.10 -0.05 0.03 -0.02
25 -0.09 -0.16 -0.11 -0.12 -0.02 0.08 0.01 -0.11 -0.06 0.03
24 0.06 0.11 -0.13 -0.11 -0.01 0.08 -0.07 -0.03 -0.08 -0.06
23 0.00 -0.03 0.11 -0.06 -0.43 -0.13 0.00 -0.03 0.00 -0.04
22 0.18 -0.10 -0.02 0.22 -0.19 -0.24 -0.22 -0.14 0.02 0.09
21 0.04 0.07 -0.02 0.14 0.49 0.10 0.00 -0.29 -0.16 0.01
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111

Chart 44.--Wind stress curl for August.

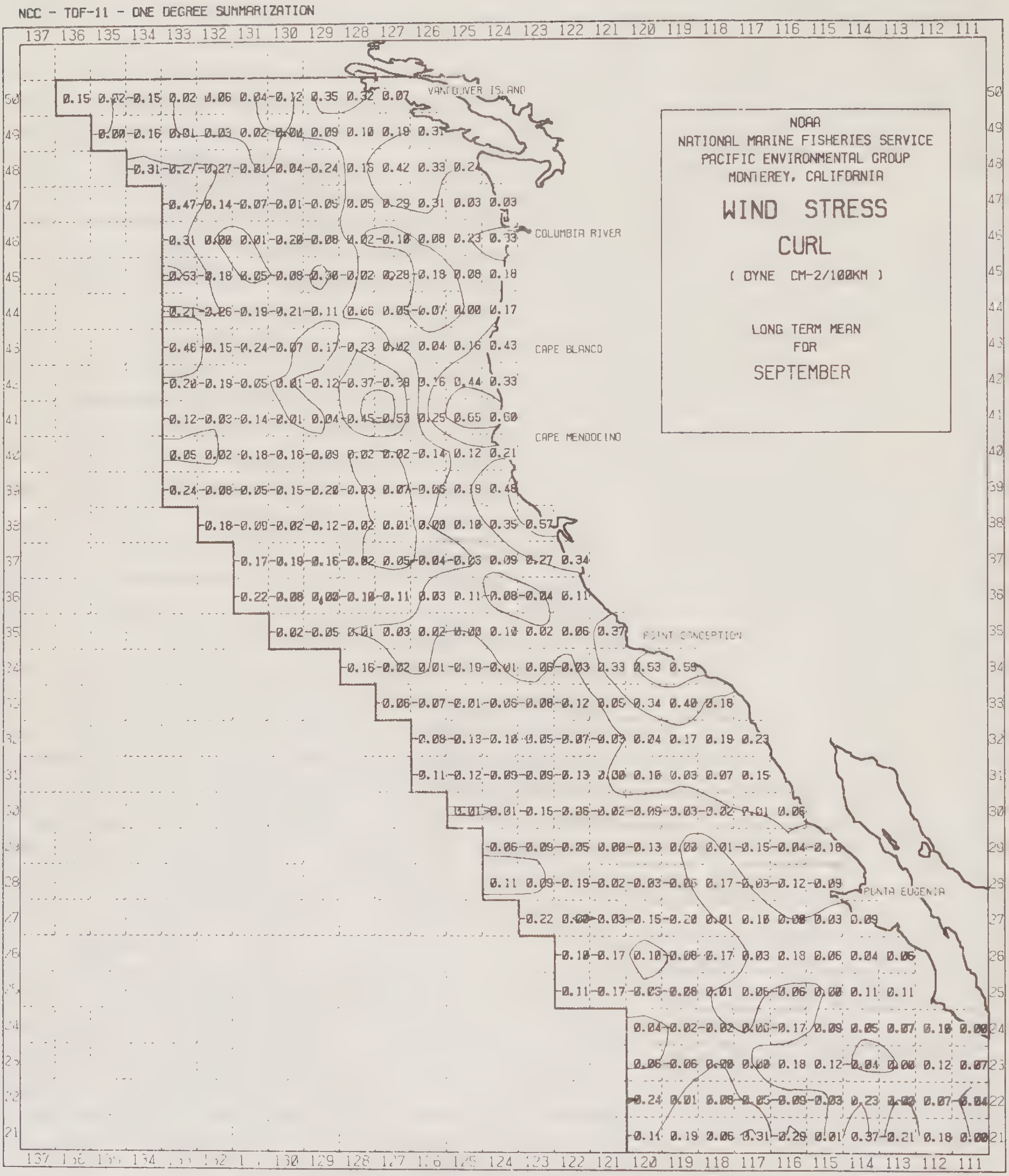
NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
WIND STRESS
CURL
(DYNE CM-2/100KM)
LONG TERM MEAN
FOR
SEPTEMBER
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
0.15 0.02 -0.15 0.02 0.06 0.04 -0.12 0.35 0.32 0.07
-0.00 -0.16 0.01 0.03 0.02 0.04 0.09 0.10 0.19 0.31
-0.31 -0.27 -0.27 -0.01 -0.04 -0.24 0.15 0.42 0.33 0.2
-0.47 -0.14 -0.07 -0.01 -0.05 0.05 0.29 0.31 0.03 0.03
-0.31 0.00 0.01 -0.20 -0.08 0.02 -0.10 0.08 0.23 0.33
-0.53 -0.18 0.05 -0.08 -0.30 -0.02 0.28 -0.18 0.08 0.18
0.21 -0.26 -0.19 -0.21 -0.11 0.06 0.05 -0.07 0.00 0.17
-0.46 0.15 -0.24 -0.07 0.17 -0.23 0.02 0.04 0.16 0.43
-0.20 -0.19 -0.05 0.01 -0.12 -0.37 -0.39 0.16 0.44 0.33
-0.12 -0.03 -0.14 -0.01 0.04 -0.45 -0.53 0.25 0.65 0.60
0.05 0.02 -0.18 -0.18 -0.09 0.02 0.02 -0.14 0.12 0.21
-0.24 -0.08 -0.05 -0.15 -0.20 -0.03 0.07 -0.06 0.19 0.48
-0.18 -0.09 -0.02 -0.12 -0.02 0.01 0.00 0.10 0.35 0.57
-0.17 -0.19 -0.16 -0.02 0.05 -0.04 -0.25 0.09 0.27 0.34
-0.22 -0.08 0.00 -0.10 -0.11 0.03 0.11 -0.08 -0.04 0.11
-0.02 -0.05 0.01 0.03 0.02 -0.00 0.10 0.02 0.06 0.37
-0.16 -0.02 0.01 -0.19 -0.01 0.06 -0.03 0.33 0.53 0.59
-0.06 -0.07 -0.01 -0.06 -0.08 -0.12 0.05 0.34 0.40 0.18
-0.08 -0.13 -0.10 0.05 -0.07 -0.03 0.24 0.17 0.19 0.23
-0.11 -0.12 -0.09 -0.09 -0.13 0.00 0.16 0.03 0.07 0.15
0.01 -0.01 -0.15 -0.36 -0.02 -0.09 -0.03 -0.02 0.01 0.06
-0.06 -0.09 -0.05 0.00 -0.13 0.00 0.01 -0.15 -0.04 -0.10
0.11 0.09 -0.19 -0.02 -0.03 -0.06 0.17 -0.03 -0.12 -0.09
-0.22 0.00 -0.03 -0.15 -0.20 0.01 0.10 0.00 0.03 0.09
-0.10 -0.17 0.10 -0.08 0.17 0.03 0.18 0.06 0.04 0.06
-0.11 -0.17 -0.25 -0.08 0.01 0.06 -0.06 0.00 0.11 0.11
0.04 -0.02 -0.02 0.06 -0.17 0.09 0.05 0.07 0.10 0.00
0.06 -0.06 0.00 0.00 0.18 0.12 -0.04 0.00 0.12 0.07
-0.24 0.01 0.08 -0.05 -0.09 -0.03 0.23 0.00 0.07 -0.04
-0.11 0.19 0.06 -0.31 -0.29 0.01 0.37 -0.21 0.18 0.00

Chart 45.—Wind stress curl for September.

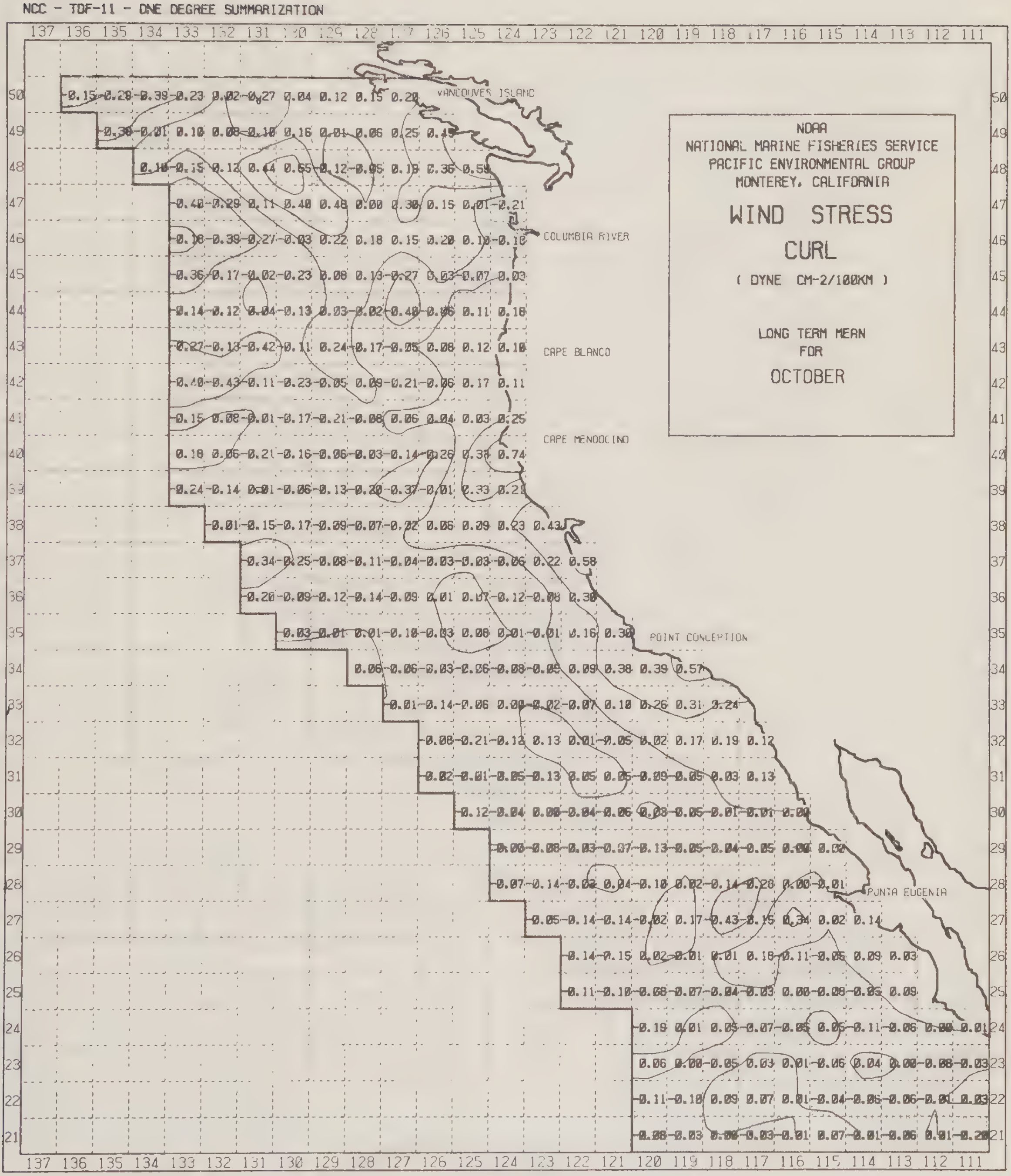
NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
WIND STRESS
CURL
(DYNE CM-2/100KM)
LONG TERM MEAN
FOR
OCTOBER
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
-0.15 -0.28 -0.39 -0.23 0.02 -0.27 0.04 0.12 0.15 0.20
-0.30 -0.01 0.10 0.08 -0.10 0.16 0.01 0.06 0.25 0.45
0.10 -0.15 0.12 0.44 0.65 -0.12 -0.05 0.18 0.36 0.59
-0.40 -0.29 0.11 0.40 0.48 0.00 0.30 0.15 0.01 -0.21
-0.18 -0.39 -0.27 -0.03 0.22 0.18 0.15 0.20 0.10 -0.10
-0.36 -0.17 -0.02 -0.23 0.08 0.13 -0.27 0.03 -0.07 0.03
-0.14 -0.12 0.04 -0.13 0.03 -0.02 -0.40 -0.06 0.11 0.10
-0.27 -0.13 -0.42 -0.11 0.24 -0.17 -0.05 0.08 0.12 0.10
-0.40 -0.43 -0.11 -0.23 -0.05 0.09 -0.21 -0.06 0.17 0.11
-0.15 0.08 -0.01 -0.17 -0.21 -0.08 0.06 0.04 0.03 0.25
0.18 0.06 -0.21 -0.16 -0.06 -0.03 -0.14 -0.26 0.38 0.74
-0.24 -0.14 0.01 -0.06 -0.13 -0.20 -0.37 -0.01 0.33 0.21
-0.01 -0.15 -0.17 -0.09 -0.07 -0.22 0.06 0.09 0.23 0.43
-0.34 -0.25 -0.08 -0.11 -0.04 -0.03 -0.03 -0.06 0.22 0.58
-0.20 -0.09 -0.12 -0.14 -0.09 0.01 0.07 -0.12 -0.08 0.30
-0.03 -0.01 0.01 -0.10 -0.03 0.08 0.01 -0.01 0.16 0.30
0.06 -0.06 -0.03 -0.06 -0.08 -0.05 0.09 0.38 0.39 0.57
-0.01 -0.14 -0.06 0.00 -0.02 -0.07 0.10 0.26 0.31 0.24
-0.08 -0.21 -0.12 0.13 0.01 -0.05 0.02 0.17 0.19 0.12
-0.02 -0.01 -0.05 -0.13 0.05 0.05 -0.09 -0.05 0.03 0.13
-0.12 -0.04 0.00 -0.04 -0.06 0.03 -0.05 -0.01 -0.01 0.00
0.00 -0.08 -0.03 -0.37 -0.13 -0.05 -0.04 -0.05 0.00 0.02
-0.07 -0.14 -0.03 0.04 -0.10 0.02 -0.14 -0.28 0.00 -0.01
-0.05 -0.14 -0.14 -0.02 0.17 -0.43 -0.15 0.34 0.02 0.14
-0.14 -0.15 0.02 -0.01 0.01 0.18 -0.11 -0.06 0.09 0.03
-0.11 -0.10 -0.08 -0.07 -0.04 -0.03 0.00 -0.08 -0.05 0.09
-0.19 0.01 0.05 -0.07 -0.05 0.05 -0.11 -0.06 0.00 0.01
0.06 0.00 -0.05 0.03 0.01 -0.06 0.04 0.00 -0.08 -0.03
-0.11 -0.10 0.09 0.07 0.01 -0.04 -0.06 -0.06 -0.01 0.03
-0.08 -0.03 0.00 -0.03 -0.01 0.07 -0.01 -0.06 0.01 -0.20

Chart 46.—Wind stress curl for October.

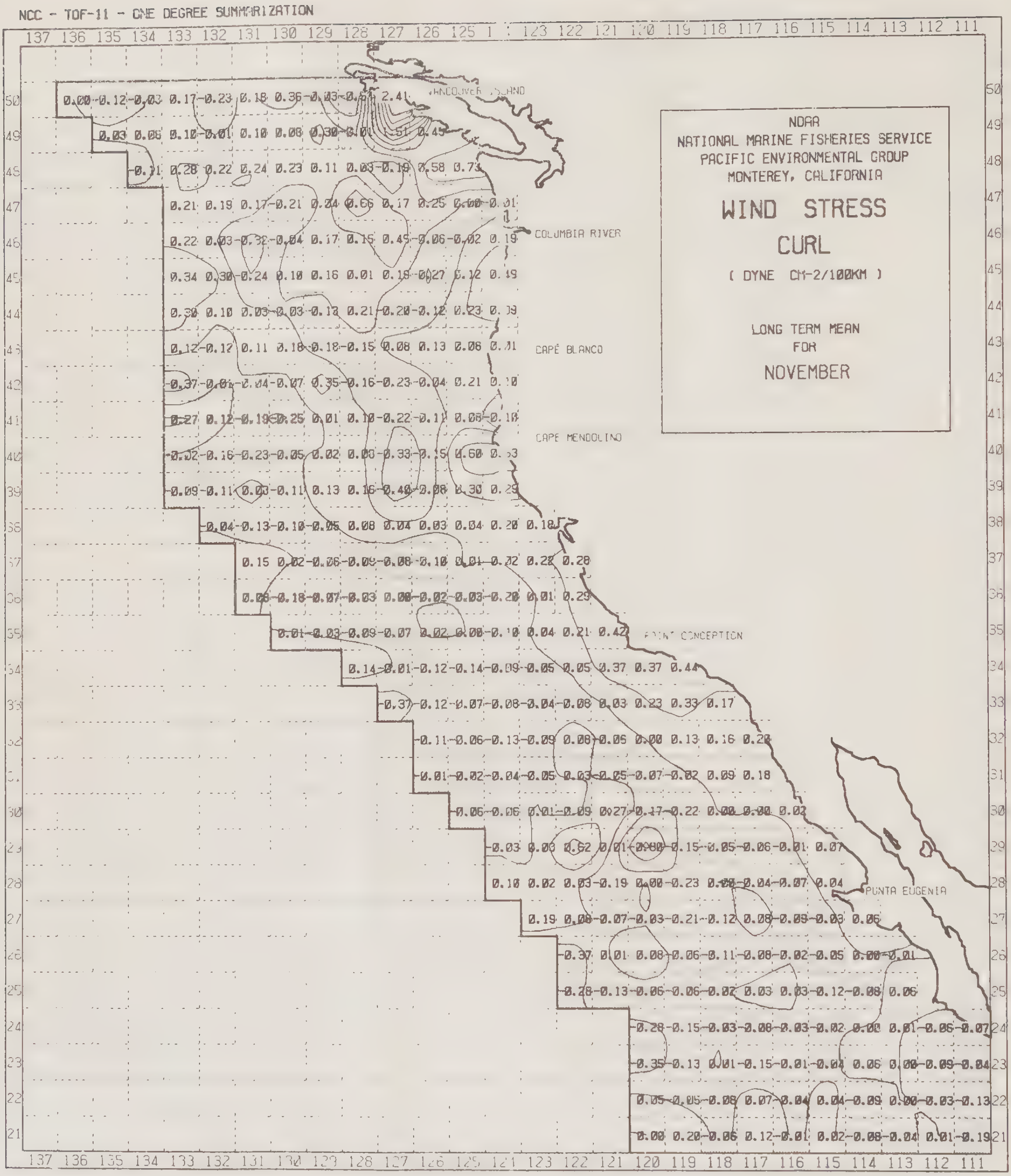
NCC - TOF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
WIND STRESS
CURL
(DYNE CM-2/100KM)
LONG TERM MEAN
FOR
NOVEMBER
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
0.00 -0.12 -0.03 0.17 -0.23 0.18 0.36 -0.03 -0.5 2.41
0.03 0.05 0.10 -0.01 0.10 0.08 0.30 -0.01 1.51 0.45
-0.11 0.28 0.22 0.24 0.23 0.11 0.03 -0.19 0.58 0.73
0.21 0.19 0.17 -0.21 0.24 0.66 0.17 0.25 0.00 -0.01
0.22 0.03 -0.32 -0.04 0.17 0.15 0.45 -0.06 -0.02 0.19
0.34 0.30 -0.24 0.10 0.16 0.01 0.18 -0.27 0.12 0.49
0.30 0.10 0.03 -0.03 -0.13 0.21 -0.20 -0.12 0.23 0.39
0.12 -0.17 0.11 0.18 -0.18 -0.15 0.08 0.13 0.06 0.01
-0.37 -0.01 -0.04 -0.07 0.35 -0.16 -0.23 -0.04 0.21 0.10
0.27 0.12 -0.19 -0.25 0.01 0.10 -0.22 -0.11 0.08 -0.10
-0.02 -0.16 -0.23 -0.05 0.02 0.00 -0.33 -0.15 0.60 0.53
-0.09 -0.11 0.03 -0.11 0.13 0.16 -0.40 -0.08 0.30 0.29
-0.04 -0.13 -0.10 -0.05 0.08 0.04 0.03 0.04 0.20 0.18
0.15 0.02 -0.06 -0.09 -0.08 -0.10 0.01 -0.02 0.22 0.28
0.08 -0.18 -0.07 -0.03 0.00 -0.02 -0.03 -0.20 0.01 0.29
-0.01 -0.03 -0.09 -0.07 0.02 0.00 -0.10 0.04 0.21 0.42
0.14 -0.01 -0.12 -0.14 -0.09 -0.05 0.05 0.37 0.37 0.44
-0.37 -0.12 -0.07 -0.08 -0.04 -0.08 0.03 0.23 0.33 0.17
-0.11 -0.06 -0.13 -0.09 0.08 -0.05 0.00 0.13 0.16 0.20
-0.01 -0.02 -0.04 -0.05 0.03 -0.05 -0.07 -0.02 0.09 0.18
-0.06 -0.06 0.01 -0.09 0.27 -0.17 -0.22 0.00 0.00 0.02
-0.03 0.03 0.62 0.01 -0.00 -0.15 -0.05 -0.06 -0.01 0.07
0.10 0.02 0.03 -0.19 0.00 -0.23 0.00 -0.04 -0.07 0.04
0.19 0.00 -0.07 -0.03 -0.21 -0.12 0.08 -0.09 -0.03 0.06
-0.37 0.01 0.08 -0.06 -0.11 -0.08 -0.02 -0.05 0.00 -0.01
-0.28 -0.13 -0.06 -0.06 -0.02 0.03 0.03 -0.12 -0.08 0.06
-0.28 -0.15 -0.03 -0.08 -0.03 -0.02 0.00 0.01 -0.06 -0.07
-0.35 -0.13 0.01 -0.15 -0.01 -0.04 0.06 0.00 -0.09 -0.04
0.05 -0.05 -0.08 0.07 -0.04 0.04 -0.09 0.00 -0.03 -0.13
0.00 0.20 -0.06 0.12 -0.01 0.02 -0.08 -0.04 0.01 -0.19

Chart 47.—Wind stress curl for November.

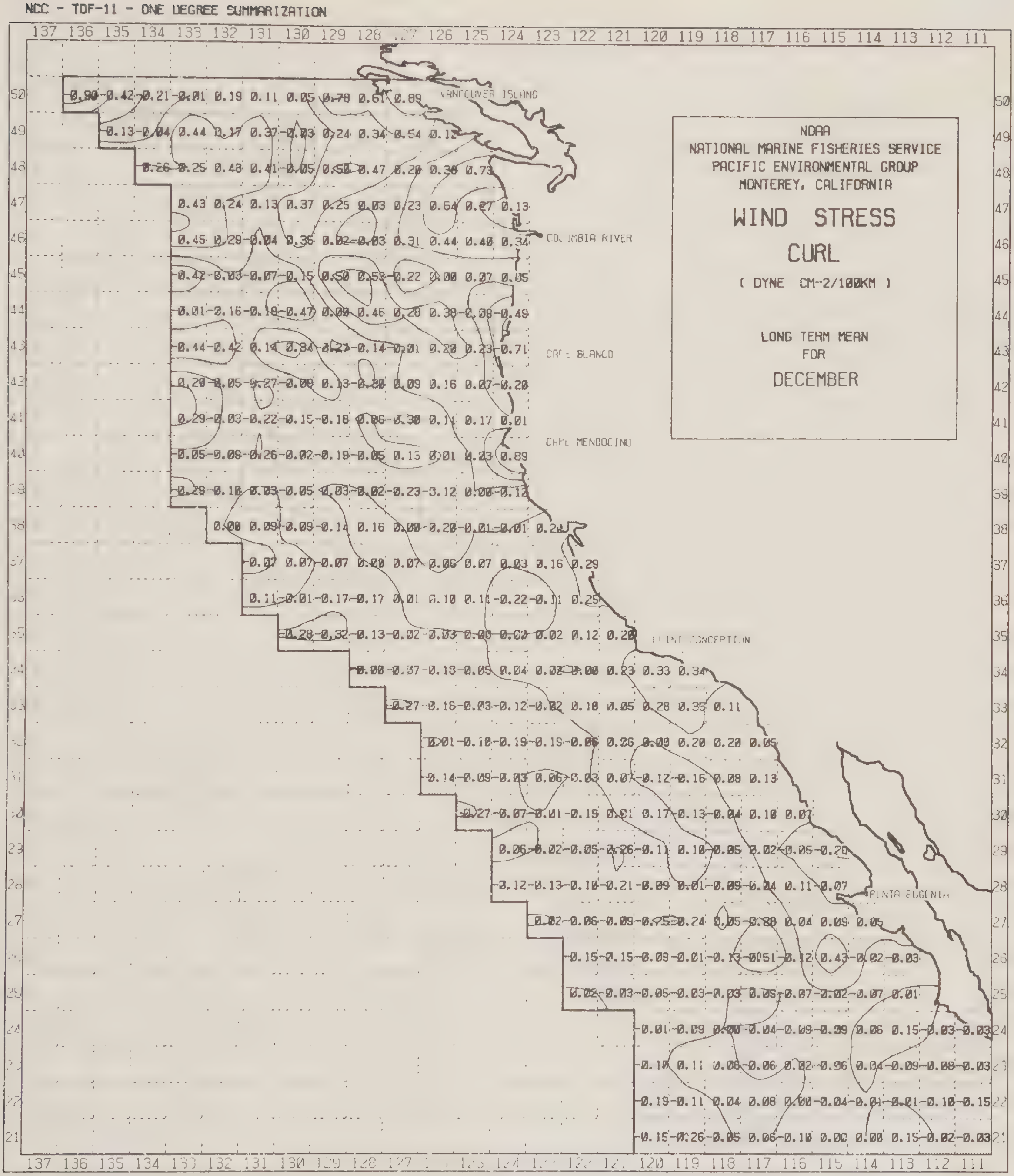
NCC - TDF-11 - ONE DEGREE SUMMARIZATION
137 136 135 134 133 132 131 130 129 128 127 126 125 124 123 122 121 120 119 118 117 116 115 114 113 112 111
50 49 48 47 46 45 44 43 42 41 40 39 38 37 36 35 34 33 32 31 30 29 28 27 26 25 24 23 22 21
NOAA
NATIONAL MARINE FISHERIES SERVICE
PACIFIC ENVIRONMENTAL GROUP
MONTEREY, CALIFORNIA
WIND STRESS
CURL
(DYNE CM-2/100KM)
LONG TERM MEAN
FOR
DECEMBER
VANCOUVER ISLAND
COLUMBIA RIVER
CAPE BLANCO
CAPE MENDOCINO
POINT CONCEPTION
PUNTA EUGENIA
-0.80-0.42-0.21-0.01 0.19 0.11 0.05 0.70 0.61 0.89
-0.13-0.04 0.44 0.17 0.37-0.03 0.24 0.34 0.54 0.12
-0.26-0.25 0.48 0.41-0.05 0.50 0.47 0.20 0.38 0.73
0.43 0.24 0.13 0.37 0.25 0.03 0.23 0.64 0.27 0.13
0.45 0.29-0.04 0.35 0.02-0.03 0.31 0.44 0.40 0.34
-0.42-0.03-0.07-0.15 0.50 0.53-0.22 0.00 0.07 0.05
-0.01-0.16-0.19-0.47 0.00 0.46 0.28 0.38-0.08-0.49
-0.44-0.42 0.19 0.34-0.27-0.14-0.01 0.20 0.23-0.71
0.20-0.05-0.27-0.00 0.13-0.20 0.09 0.16 0.07-0.20
0.29-0.03-0.22-0.15-0.18 0.06-0.30 0.11 0.17 0.01
-0.05-0.09-0.26-0.02-0.19-0.05 0.15 0.01 0.23 0.89
-0.29-0.10 0.03-0.05 0.03-0.02-0.23-0.12 0.00-0.12
0.00 0.09-0.09-0.14 0.16 0.00-0.20-0.01-0.01 0.26
-0.07 0.07-0.07 0.00 0.07-0.06 0.07 0.03 0.16 0.29
0.11-0.01-0.17-0.17 0.01 0.10 0.11-0.22-0.11 0.25
-0.28-0.32-0.13-0.02-0.03 0.00-0.02 0.02 0.12 0.20
-0.00-0.37-0.13-0.05 0.04 0.02-0.00 0.23 0.33 0.34
-0.27-0.16-0.03-0.12-0.02 0.10 0.05 0.28 0.35 0.11
-0.01-0.10-0.19-0.19-0.06 0.26 0.09 0.20 0.20 0.05
-0.14-0.09-0.03 0.06-0.03 0.07-0.12-0.16 0.08 0.13
-0.27-0.07-0.01-0.19 0.01 0.17-0.13-0.04 0.10 0.07
0.06-0.02-0.05-0.26-0.11 0.10-0.05 0.02-0.05-0.20
-0.12-0.13-0.10-0.21-0.09 0.01-0.09-0.04 0.11-0.07
0.02-0.06-0.09-0.75-0.24 0.05-0.80 0.04 0.09 0.05
-0.15-0.15-0.09-0.01-0.13-0.51-0.12 0.43-0.02-0.03
0.02-0.03-0.05-0.03-0.03 0.05-0.07-0.02-0.07 0.01
-0.01-0.09 0.00-0.04-0.09-0.09 0.06 0.15-0.03-0.03
-0.10 0.11 0.08-0.06 0.02-0.96 0.04-0.09-0.08-0.03
-0.19-0.11 0.04 0.08 0.00-0.04-0.01-0.01-0.10-0.15
-0.15-0.26-0.05 0.06-0.10 0.00 0.00 0.15-0.02-0.03

Chart 48.—Wind stress curl for December.

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遠洋水研と私
マグロ研究の思い出 -

米国海洋漁業局ホノルル水産研究所
Tamio OTSU

私がホノルル水産研究所で漁業生物学の研究をはじめることになったのは、1950年にさかのぼりますが、それ以来の長い年月をかえりみて、私の研究歴が遠洋水産研究所（その前には南海区水産研究所）といかに密接なかかわりをもっていたかを思い、感慨深いものがあります。

私のマグロ研究歴のそもそもの始まりから、日本の高知にあった南海水研で刊行される研究報告に依ることが多大でありました。いろいろな研究報告を読んでいくうちに、矢部、行縄、渡辺、上柳、本間、上村、木川、中村、須田、新宮、山中（一）、山中（一郎）、薮田、三村、……の名前が私に親しいものとなりました。

マグロの分布や生物学の知識が次第に増してくるうちに、私は、1951年に、日本のマグロ母船（大洋漁業の第三天洋丸）にオブザーバーとして出向を命じられました。そのマグロ母船団の操業海域は米国の信託統治領を含む水域で、マグロ漁場開拓のために16隻のキャッチャーを伴ったものでした。私の立場は、米国の魚類野生生物局（現在の海洋漁業局）、米国海軍、とそれに米国信託統治領の高等弁務官の代表といったものでした。主要な目的は、マグロ類の漁獲統計資料やその他の生物学的な知見を蒐集することでした。

これが私の生まれてはじめての日本訪問であり、私にとって最も thrilling な経験でした。当時、私の日本に対する唯一の関わりは、私のルーツが日本にあるということ——祖父達が昔、熊本からハワイに移住して来た——でした。マグロ母船の上で、日夜日本語と格闘し、日本式生活に慣れようと努めながら、日本のオフィサーや船員の人達の間で過した新しい経験は、私にとって素晴しいものでした。それはもうはるかな過去となりましたが、未だに、日本への最初の旅行の美しい思い出として心に残っております。

四カ月半にわたる旅行（その大部分は海の上だったのですが）からハワイに帰ってから、私は再び研究を始め、南海水研のマグロ研究報告を読むことをつづけました。

それから、1960年に、北太平洋ビンナガマグロの協同研究について中村広司所長や研究者達と話合うために、はじめて南海水研を訪問する機会が与えられ、研究所の皆さんにまみえる喜びを持ちました。その時私のおぼえていた名前と顔とをはじめて結びつけることが出来、若く活動的な研究者の姿に印象づけられました。ホノルルへ帰ってからも、通信によって、親しくなった南海水研の研究者達との交友を深めるように努めましたが、その後、何人かの友人とは、1961年にホノルルで持たれた太平洋マグロ生物学会議や、1962年にラ・ホヤで開催されたＦＡＯの世界マグロ生物学会議などで再会する機会を得ました。

この時点で、私や私の同僚にとって、マグロ類の生物学や分布等の知見に関する重要な貢献の多くが、南海水研の研究者達によって遂行されている研究に由来していることがはっきりして来まして、私と南海水研のスタッフとの関係は更に年々緊密さを加えて来ました。地理的には離れていても、私は、本当に、日本のマグロ研究者達と共に成長して来たと思います。

私にとって忘れられないもう一つの経験は、ビンナガ研究のために再び南海水研を訪れ、6カ月間高知に滞在したことでした。それは丁度東京オリンピックのあった1964年で、その時は妻と二人の娘を同伴しました。高知市の郊外の万々というところに家を借り、子供達は高知の小学校に通いました。妻は多勢の友人が出来、特にスーパーマーケットや商店の人達と親しくなり、子供達も学校友達からとても親切にしてもらいました。南海水研のスタッフや、その家族の人達は、私たちの高知滞在が快適なものとなるように、何でもしてくれましたし、研究所での仕事がよく出来るように協力してくれました。私たちが高知を去る日に、高知駅に見送りに来てくれた多勢の方達の写真をたびたび出して眺めることがあります。私たちは、また、子供達のために学校の先生、校長先生、クラスメートの皆さんが、お別れの言葉を吹きこんでくれたテープを大切に保存しています。これらの思い出の数々は、私の南海水研以来の友人に対する信頼の気持に深く結びついています。

遠洋水研とホノルル水研の間も、当初から今日まで緊密な関係がつづけられて来ました。共同研究計画（北太平洋ビンナガ資源研究）を実施してくることが出来ましたし、非公式なものではありますが、〝姉妹研究所〟の関係をもってきました。両研究所が共通の問題や関心、利益のもとに研究を進めて来たわけですから、これは自然の成行きだったといえましょう。両研究所の緊密な関係を維持、発展させることに役立つために、私が〝橋渡し〟の役目を果してくることが出来ましたことを幸いに思っております。両研究所が今や太い絆で結ばれていることは疑いないことです。私は、遠洋水研が世界の指導的なマグロ研究所の一つとして確立されていることを信じ、また我々のホノルル水研もこの分野で同様な評価を受けることを願っております。

遠洋 特集号 (August, 1977)

私の多くの日本の友達は、〝ミスター・オーツは、日本語で考え、日本人をよく理解しているので、話が通じ易い〟と言ってくれますが、これは私にとって大変嬉しいことです。私自身、ハワイにおいて役立ち、また日本との関係においてもそうであるために、日本語と日本のことを一生懸命学んできました。皆さんが言って下さるようにこの分野で私も若干の進歩があったと思います。また、遠洋水研の友人達を核として、私は日本における友情の輪を拡げることが出来ました。マグロ研究の関係だけでなく、いろいろな方面の人達と友人になり、今では日本のどこへ行っても、友達に会うことが出来ます。

ホノルル水研での私のキャリアーがだんだん終りに近づきつつありますが、ふりかえって、今日まで、ハワイにおける私の仕事がより有益なものとなるために、遠洋水研の皆さんがして下さった全てのことに、感謝するものであります。

私たちの研究所にもいろいろと変化があり、何回も機構改革を経験して来ました。遠洋水研も、矢部さん、木部崎さん、福田さんと所長さんがかわられ、種々の変化を経て来られたことと思いますが、私の皆さんに対する心からの友情と尊敬は全ての変化を通しても変らないものでした。遠洋水研発足10周年を記念しての「遠洋ニュース」特集号に、日本の友人に対する私の真情を述べるよい機会を与えられましたことを深く感謝します。本当にありがとうございました。

遠洋水研の今後益々の御発展を期待し、ホノルル水研との緊密な関係がつづけられますよう願っております。

A STATEMENT FOR INCLUSION IN THE FAR SEAS
FISHERIES RESEARCH LABORATORY 10TH ANNIVERSARY
SPECIAL EDITION OF THEIR LABORATORY NEWSLETTER
(to appear in Japanese)

THE FAR SEAS FISHERIES RESEARCH LABORATORY AND I--RECOLLECTIONS ON TUNA RESEARCH

By

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My career in fishery biology at the Honolulu Laboratory began in 1950. It is interesting to look back on the many years that have passed since, and to see how closely my career has been tied in with the Far Seas Fisheries Research Laboratory (formerly Nankai Regional Fisheries Research Laboratory).

From the very beginning of my career in studying tunas, I began to rely to a large degree on published reports from the Nankai Laboratory in Kochi, Japan. Many names became very familiar to me from studying the various publications from the Laboratory: Yabe, Yukinawa, Watanabe, Ueyanagi, Honma, Kamimura, Kikawa, Nakamura, Suda, Shingu, Yamanaka Hajime, Yamanaka Ichiro, Yabuta, Mimura, etc. After acquainting myself with available information on tuna biology and tuna distribution, I was assigned to go to Japan in 1951 to serve as an observer on a Japanese tuna mothership (No. 3 Tenyo Maru of the Taiyo Fishing Company) which accompanied a fleet of 16 catcher vessels to waters of the U.S. Trust Territory on a tuna fishing expedition. I went as a representative of the U.S. Fish and Wildlife Service (presently the National Marine Fisheries Service), the U.S. Navy, and the High Commissioner of the U.S. Trust Territory. My primary mission was to collect tuna catch and effort data and other biological information. It was my very first visit to Japan, and I must admit, a most thrilling experience. At that time my only claim to Japan was that I was of Japanese extraction; my grandparents had emigrated to Hawaii from Kumamoto Prefecture many years ago. It was a wonderful new experience working among Japanese officers and crews of the mothership and the catcher vessels, struggling to speak Japanese and acquainting myself with Japanese customs. I still have beautiful memories of this first excursion to Japan. That was a long time ago.

Upon returning to Hawaii after the 4-1/2 month trip, most of which was unfortunately spent at sea, I resumed my studies and continued reading reports originating from the Nankai Laboratory. In 1960 I visited the Nankai Laboratory for the first time, for the purpose of discussing with Dr. Hiroshi Nakamura and his staff, a cooperative North Pacific albacore study. It was then that I had the pleasure of meeting the entire staff of the Nankai Laboratory. I was impressed by the young and energetic staff and for the first time I was able to associate faces with the many familiar names. After my return to Honolulu I continued to nurture the friendships I had developed with the Nankai Laboratory staff through correspondence, and later met several of them again at the Honolulu Tuna Biology Conference in 1961 and again at the FAO World Scientific Meeting on the Biology of Tunas and Related Species held in La Jolla in 1962. By this time, it was very clear to me and my colleagues that much of the important contributions to the knowledge of tuna biology and distribution originated from studies conducted by scientists of the Nankai Laboratory. My relationship with the staff of that Laboratory grew closer and closer over the years. In a real sense, though separated geographically, I have grown up together with most of the tuna scientists who are now at the Far Seas Laboratory in Shimizu.

Another experience I shall never forget is when my work on albacore took me to Japan for a 6-month visit to the Nankai Laboratory. This was in 1964, the year of the Tokyo Olympics. On this trip I was accompanied by my wife and two daughters. We rented a house in the outskirts of Kochi City at Mama, and my two children attended Kochi Elementary School. My wife made many friends, particularly in the city's supermarkets and shops, while my children were treated very well by their classmates. The staff of the Nankai Laboratory, and their families, did everything possible to make our stay in Kochi comfortable and to help me get my work done at the Laboratory. I frequently look at the photographs showing the large numbers of people who came to see us off at the train station on the day of our departure. We also treasure a tape recording in which everyone in our two children's classes, including the teachers and principal, recorded their farewell messages. These remembrances tie in very intimately with the deep feelings I have for the people of the Nankai Laboratory.

The relationship between the Far Seas Laboratory and the Honolulu Laboratory has remained very close over these many years. We have been able to work together on cooperative projects; we have essentially established a "sister laboratory" relationship, though on an informal basis. This is perhaps a natural development, since our laboratories have worked on common problems, of mutual interest and benefit. I am happy that I have been able to serve in the role of "liaison" between our laboratories in helping to develop and to maintain such a close working relationship. There certainly is no denying the fact that a great bond has developed between our two laboratories. I believe that the Far Seas Laboratory has established itself as one of the leading tuna laboratories in the world. We hope that the Honolulu Laboratory is held in equally high esteem by our colleagues in this field.

Many of my Japanese friends have remarked that "Mr. Otsu thinks Japanese, and understands the Japanese people, and therefore it is easy to relate to him." This makes me very happy. Nothing could possibly make me happier than to be regarded in this manner. I have studied Japanese and things Japanese in order to be able to serve a useful purpose in Hawaii and in our relationship with the Japanese. From your many comments, I must assume that I have achieved some measure of success in this area. Through a fine nucleus of friends at the Far Seas Laboratory, I have enlarged my circle of friends throughout Japan, not only with those related to work on tunas, but to other fisheries as well, and today, I am able to visit nearly everywhere in Japan and expect to meet some old friends.

As I approach the end of my career with the Honolulu Laboratory, I can look back and appreciate everything you at the Far Seas

Laboratory have done for me to make my work in Hawaii more meaningful and useful. We have gone through many changes, many reorganizations, just as you have. I have seen your Laboratory go through a succession of directors: Nakamura, Takashiba, Yabe, Kibezaki, and Fukuda. My deep feeling of friendship and regard for you has remained unaltered through all these changes. I thank you very much for inviting me to express my thoughts and feelings to you in your special 10th Anniversary Edition of the Enyo Newsletter.

I am proud that many of my Japanese friends have labeled me a "Junsui no Nippon-Jin." What greater compliment can I expect? Thank you very much. I look forward to many more productive years for the Far Seas Laboratory and to continued close relationship with the Honolulu Laboratory.

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GROWTH AND REPRODUCTION OF THE EASTERN SPINNER DOLPHIN, A GEOGRAPHICAL FORM OF *STENELLA LONGIROSTRIS* IN THE EASTERN TROPICAL PACIFIC

William F. Perrin, David B. Holts, and Ruth B. Miller[1]

ABSTRACT

Estimates of life history parameters for use in assessing status of the population of the eastern spinner dolphin and assessing impact of incidental mortality in the yellowfin tuna fishery are developed from data on 2,675 specimens collected from 1968 to 1975. Average length at birth is 77.0 cm, gestation is 10.6 mo, average length at 1 yr is approximately 134 cm. Three alternative hypotheses of rate of deposition of dentinal growth layers are: I) 1.5 layers/yr throughout life; II) 1.5 layers in the first year, 1/yr thereafter (most favored hypothesis); and III) 1.5 layers until puberty (at 5.5 layers in females and 9 layers in males), and 1/yr thereafter. Males attain sexual maturity on the average at about 170 cm (range 160–195) and 9–12 layers (6.0–11.5 yr), depending on the criterion of testis–epididymis weight chosen. Average length at attainment of social maturity is unknown. Average length of adult males is 174–176 cm. Females on the average attain sexual maturity at 165 cm (5.5 layers or 3.7, 5.0, or 3.7 yr under Hypotheses I, II, and III). Average length of sexually adult females is 171 cm (range 152–187). Ovulation rate is 1/growth layer (1/0.67–1.00 yr) until about 10 ovarian corpora have been accumulated, after which the rate declines. Approximately 1% of adult females are postreproductive. Best estimates of annual pregnancy rate range from 0.450 (based on 1973 data) to 0.474 (based on 1974 data). The pooled estimate for all years' data is 0.461. The corresponding estimates of calving interval (reciprocal of pregnancy rate) are 2.22 yr, 2.11 yr, and 2.17 yr, respectively. Pregnancy rate decreases after age of about 12 layers (8.0, 11.5, or 10.2 yr) concomitant with increase in lactation rate. Overall sex ratio is near parity, but there are about 6% more females than males in adults. Best estimates of gross annual reproductive rate based on the 1973, 1974, and 1975 data are 0.099, 0.103, and 0.105, respectively. The estimate based on pooled data for the 3 yr is 0.102. The estimates are compared with estimates for the spotted dolphin, *Stenella attenuata*, and for other cetaceans.

This paper presents the results of a study of the life history of the eastern spinner dolphin, a geographical form[2] of *Stenella longirostris* (Gray 1828), in the eastern tropical Pacific. The eastern spinner dolphin accounted for the second-highest level of incidental mortality in the purse seine fishery for yellowfin tuna, *Thunnus albacares,* in the eastern Pacific through 1975, after the offshore spotted dolphin, a form of *S. attenuata* (Gray 1846) (Perrin 1969, 1975a; Perrin et al.[3]) The purpose of the study was to develop estimates of life history parameters for use in assessing the status of the eastern spinner dolphin stock and the impact on the stock of incidental mortality in the yellowfin tuna fishery. Preliminary results of partially completed analyses reported here in full appeared in Perrin et al.[4]

Very little previously published information is available on growth and reproduction of the pantropically distributed *S. longirostris.* Cadenat and Doutre (1959) listed body weights and gonadal

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[1] Southwest Fisheries Center, National Marine Fisheries Service, NOAA, P.O. Box 271, La Jolla, CA 92038.

[2] Perrin (1975b) gave the eastern spinner dolphin subspecific rank but stated that the nomenclature is not yet resolved, because the holotype of the species is from an unknown locality. The term "geographical form" is used here as a substitute for the more unwieldy "[*Stenella longirostris*] subspecies (unnamed)." The term "dolphin" is used in conformance with the "list of smaller cetaceans recognized" adopted by the Subcommittee on Smaller Cetaceans, Scientific Committee, International Whaling Commission (Anonymous 1975).

[3] Perrin, W. F., T. D. Smith, and G. T. Sakagawa. 1974. Status of populations of spotted dolphin, *Stenella attenuata*, and spinner dolphin, *Stenella longirostris,* in the eastern tropical Pacific. Working Document for Meeting of Ad Hoc Consultants Group on Small Cetaceans and Sirenians (Ad Hoc Group 2), Working Party on Marine Mammals, Advisory Committee of Experts on Marine Resources Research (ACMRR) of the Food and Agriculture Organization of the United Nations, La Jolla, Calif., December 16–19, 1974. SWFC Admin. Rep. LJ-74-42, Natl. Mar. Fish. Serv., NOAA, La Jolla, Calif., 22 p. (Unpubl. rep.)

[4] Perrin, W. F., D. B. Holts, and R. B. Miller. 1975. Preliminary estimates of some parameters of growth and reproduction of the eastern spinner porpoise, *Stenella longirostris* subspecies. SWFC Admin. Rep. LJ-75-66, Natl. Mar. Fish. Serv., NOAA, La Jolla, Calif., 33 p. (Unpubl. rep.)

Manuscript accepted February 1977.
FISHERY BULLETIN: VOL. 75, NO. 4, 1977.

data for two males (1,940 and 2,040 mm) and two females (1,790 and 1,800 mm) from off Senegal in the tropical Atlantic. Layne (1965) published similar data for two males (1,845 and 1,910 mm) and one female (1,965 mm) from Florida. Pilson and Waller (1970) reported on an adult female of *S. microps* [= *S. longirostris*] 176 cm long, from the eastern Pacific. Harrison et al. (1972) published detailed length, weight, and gonadal data for 12 males (79 to 185 cm) and 21 females (86 to 188 cm) of *S. longirostris* from the eastern Pacific; five males (150 to 182 cm) and two females (169 and 179 cm) of *S. roseiventris* [= *S. longirostis*] from Hawaii; and nine specimens from the eastern Pacific, eight males (165 to 178 cm), and one female (171.5 cm) listed as "probably *S. longirostris*." In their discussion of growth and reproduction, however, they did not differentiate between *S. longirostris* and *S. graffmani* [= *S. attenuata*], a larger species that differs significantly from *S. longirostris* in several features of life history (compare results below with those for *S. attenuata* in Perrin et al. (1976) and Kasuya et al. (1974)).

Several recent reports emanating from the Southwest Fisheries Center, National Marine Fisheries Service (NMFS), NOAA, have dealt with the developmental components of various aspects of the life history of *S. longirostris* other than reproduction. Perrin (1972) described the development of the color pattern in eastern Pacific forms of the species. Perrin and Roberts (1972) analyzed changes in organ weights with size, based on 14 specimens. Dailey and Perrin (1973) described differences in parasite frequencies correlated with age in 19 specimens. Perrin (1975a, b) described developmental variation in morphology in the eastern Pacific and defined three geographical forms (subspecies), of differing adult size: the less-than-2-m-long "eastern spinner," the subject of this report; the slightly larger "whitebelly spinner," found farther offshore; and the "Costa Rican spinner," which is restricted to the coastal waters of Central America and attains a total length of well over 2 m.

This paper treats only the eastern spinner, the form of *S. longirostris* most heavily involved in the tuna fishery through 1975 in terms of numbers of seine net sets and numbers killed (Perrin 1975a). Some data for the whitebelly spinner are included in certain of the analyses of the eastern spinner, including those of length at birth and of brain weight relative to body length, for reasons explained below. A preliminary report on the whitebelly form of *S. longirostris* appeared in Perrin et al.[5]

METHODS AND MATERIALS

The Field Program

Nearly all of the data were collected by NMFS scientific observers aboard commercial tuna vessels. The data collection procedures were the same as previously described for the spotted dolphin (Perrin et al. 1976). Data on *S. longirostris* were collected on 1 cruise in 1968, 4 in 1971, 12 in 1972, 21 in 1973, 33 in 1974, and 30 in 1975. Some specimens were also collected in 1970 by personnel of the Inter-American Tropical Tuna Commission aboard chartered purse seiners.

The Sample

In 1971 and early 1972, when the observer program was very limited, adult female specimens were selected for dissection when available, and the samples for those periods are, therefore, biased with regard to the age and sex structures of the kill. In 1968 and on cruises from October 1972 on, no selection was practiced in determining which animals were to be examined, and those samples are assumed to be cross-sectional with respect to the kill. Fetuses were not collected in 1968.

The sample of animals for which life history data including at least, but not restricted to, sex and body length includes 2,675 specimens, 2,663 from precisely known localities (Figure 1) and 12 from imprecisely known localities, from the eastern tropical Pacific between lat. 21°N and 3°S and west to long. 117°W. Because of the seasonal nature of the tuna fishery, the sample is heavily biased toward the early months of the year, with minimal coverage of the latter part of the year and practically no specimens from the summer months (Table 1). Length-frequency distributions by 5-cm increments for males and females, including fetuses, are presented by year and month in Figures 2 and 3.

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[5] Perrin, W. F., D. B. Holts, and R. B. Miller. 1976. Preliminary estimates of some parameters of growth and reproduction of the whitebelly spinner dolphin, a geographical form of *Stenella longirostris*, in the eastern tropical Pacific. Working document submitted to Meeting of Subcommittee on Small Cetaceans, Scientific Committee, International Whaling Commission, London, 7–8 June 1976. SWFC Admin. Rep. LJ-76-12, Natl. Mar. Fish. Serv., NOAA, La Jolla, Calif., 36 p. (Unpubl. rep.)

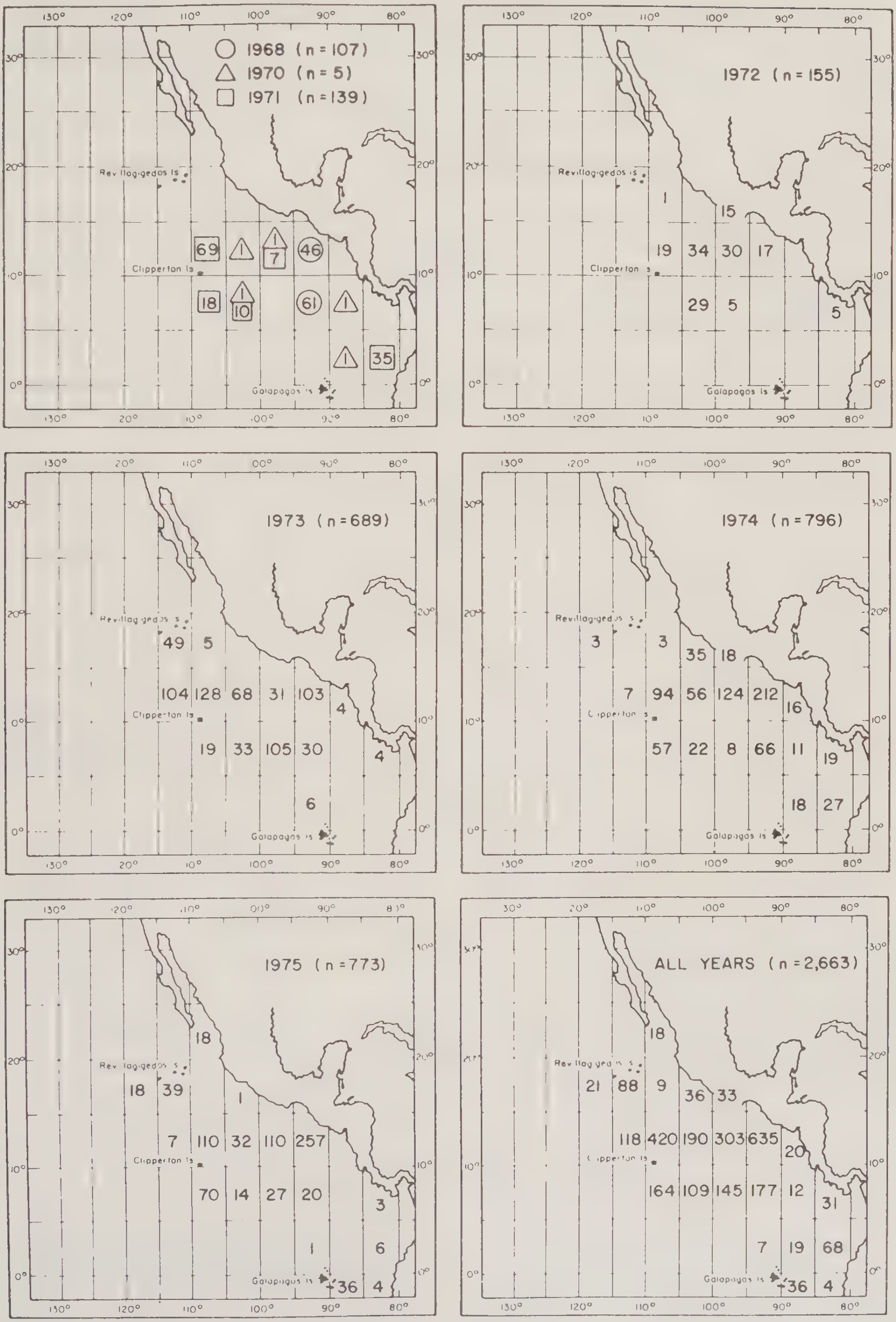
1968 (n = 107)
1970 (n = 5)
1971 (n = 139)
Rev illagigedos Is
Clipperton Is
Galapagos Is
69
1
1
7
46
18
1
10
61
1
1
35
1972 (n = 155)
1
15
19
34
30
17
29
5
5
1973 (n=689)
49
5
104
128
68
31
103
4
19
33
105
30
4
6
1974 (n=796)
3
3
35
18
7
94
56
124
212
16
57
22
8
66
11
19
18
27
1975 (n=773)
18
18
39
1
7
110
32
110
257
70
14
27
20
3
1
6
36
4
ALL YEARS (n=2,663)
18
21
88
9
36
33
118
420
190
303
635
20
164
109
145
177
12
31
7
19
68
36
4
130°
120°
110°
100°
90°
80°
30°
20°
10°
0°

FIGURE 1.—Samples of *Stenella longirostris* collected 1968-75, by 5° square.

TABLE 1.—The sample of eastern spinner dolphins used in the life history analysis, by year and month.

	1968		1970		1971[1]		1972[1]		1973		1974		1975		All years		
Month[2]	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Total
Jan.			1	2	2	11	9	12	23	24	85	104	163	170	283	323	606
Feb.					20	15		15	135	128	230	209	68	72	453	439	892
Mar.							11	35	79	78	26	18	32	31	148	162	310
Apr.	52	55					25	15	50	53	41	30	9	25	177	178	355
May							6	12	1	7	1	3	16	13	24	35	59
June												3	19	21	19	24	43
July			2										16	25	18	25	43
Aug.											3	1	12	12	15	13	28
Oct.							10	7	7	7			17	33	34	47	81
Nov.					35	39			49	45	19	27	12	9	115	120	235
Dec.					6	11			3	3					9	14	23
Total	52	55	3	2	63	76	61	96	347	345	405	395	364	411	1,295	1,380	2,675

[1] In these years, adults were selected (except in Oct. 1972). Fetuses were not collected in 1968.

[2] No samples in September.

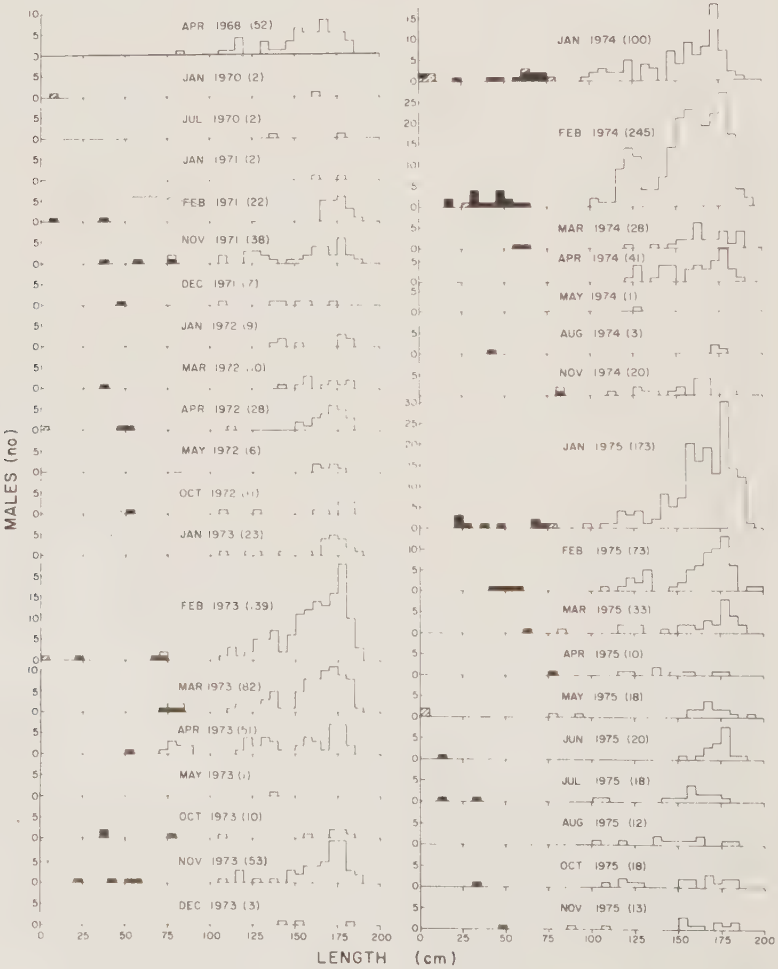

FIGURE 2.—Length-frequency distribution, by 5-cm increments, of collected male eastern spinner dolphins by year and month. Shaded squares are fetuses. Hatched squares are small fetuses of unknown sex (plotted with the males). Sample sizes in parentheses.

Laboratory Procedures

Most laboratory procedures were the same as reported for the earlier study of the growth and reproduction of the spotted dolphin (Perrin et al. 1976). The techniques used in sectioning and reading, however, differed somewhat. Some of the approximately 2,500 teeth prepared (includes recuts, multiple specimens, etc.) were sectioned with multiple cuts, using a high-speed diamond saw

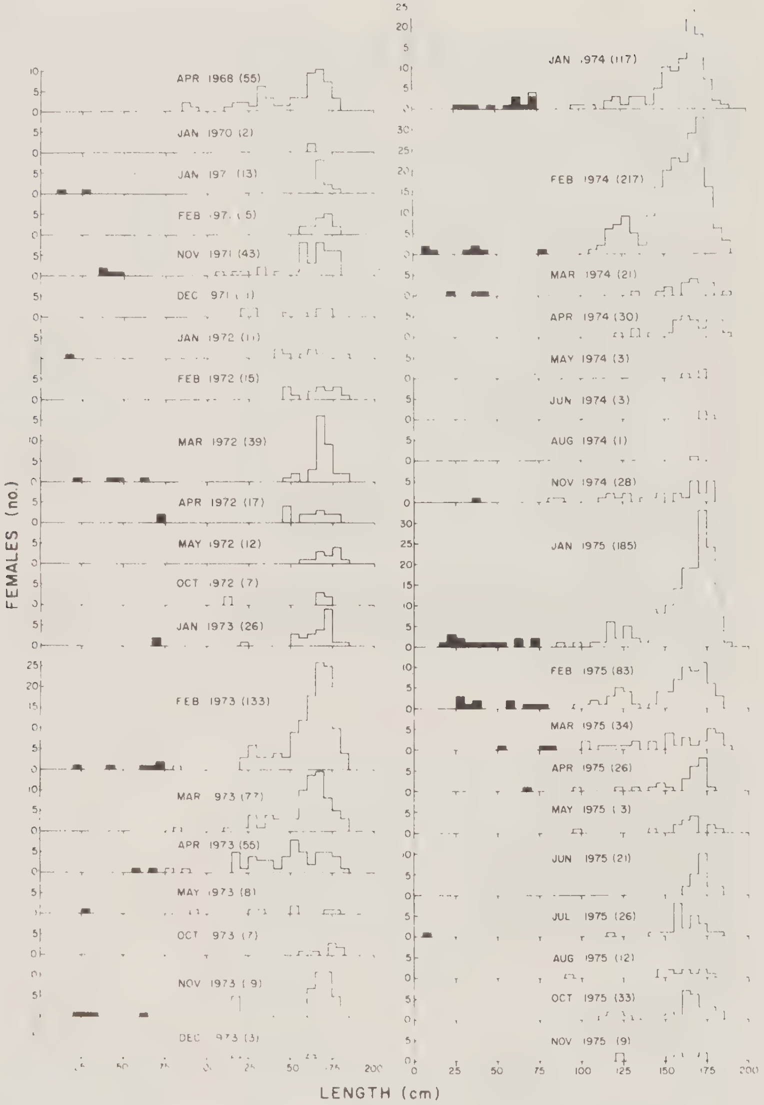

FIGURE 3.—Length-frequency distributions, by 5-cm increments, of collected female eastern spinner dolphins by year and month. Shaded squares are fetuses. Sample sizes in parentheses.

(Felker[6] model 80BQ Hi-speed Precision Cut-off Machine—36,000 rpm) with a single blade, as for *S. attenuata* (Perrin et al. 1976), but most were sectioned with a single cut of tandem blades (yielding a section of uniform 10/1,000-in thickness) with a low speed saw (Isomet model 11-1180 low speed saw—speed variable to 300 rpm). The latter method yielded sections of more uniform thickness and with fewer extraneous surface striations than did the former. After cutting, sections were immediately mounted under coverslips on microscope slides in balsam, omitting the clearing step used for the *S. attenuata* teeth. Our reading and scoring methods also differed from those in the earlier study. We found postnatal dentinal growth to be much more consistent in *S. longirostris* than in *S. attenuata* in pattern of deposition and in readability. No teeth were encountered that did not contain an open cavity, albeit in older specimens a very small one, and a smaller proportion of teeth from younger animals (<12 to 13 layers) contained convoluted secondary dentine than in *S. attenuata*. In the study of *S. attenuata*, growth layers were merely counted to the nearest half layer. In view of the better readability of the *S. longirostris* material, we felt that the approach could be refined. We measured the thickness of each growth layer on an image projected on a 16-cm diameter ground-glass screen attached to a compound microscope using dial calipers accurate to 0.1 mm. The total magnification on the screen was approximately 263 diameters. The first two layers inside the neonatal tooth were measured at approximately the same point along the length for each tooth, about halfway between the proximal end of the neonatal tooth (point where neonatal line meets outer surface) and the distal end of the neonatal pulp cavity. Layers beyond the second were measured at the place along the length of the tooth where they were most clearly defined. In converting measurements to layer units, non-innermost layers beyond the first layer were scored as full layer units regardless of thickness. The first layer, second (when innermost), and subsequent layers (when innermost) were treated differently, as follows:

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[6] Reference to trade names does not imply endorsement of the product by the National Marine Fisheries Service, NOAA.

First Layer

Cumulative percent of 417 first layers measured rapidly approaches an asymptote at approximately 0.20 mm (Figure 4). A first layer 0.20 mm thick or thicker was therefore scored as a full layer unit, and the thickness of a first layer <0.20 mm thick was divided by 0.20 mm to yield a partial layer unit.

Second Layer

In 361 teeth with three or more layers, the second layer averaged 0.145 mm thick with relatively low variance (Figure 5). In teeth with two layers, the second layer was scored as a full layer unit if 0.145 mm thick or thicker. An innermost second layer <0.145 mm thick was scored as a partial layer unit by division of the thickness by 0.145 mm.

Layers Beyond Second Layer

Full layers beyond the second layer averaged more than 95% of the thickness of the next older, adjacent layer, with considerable variation that increased toward the center of the tooth (Figure 6). We assumed, as a reasonable approximation, that complete layers beyond the third are of about the same thickness as adjacent layers, and thickness of the innermost layer in teeth with three or more layers was scored as a proportion of the next older, adjacent layer. Layer scores thus obtained were added and rounded off to the nearest tenth of a layer.

Brain weights were obtained from brains dissected out of freshly thawed heads or whole carcasses of specimens deep frozen at sea aboard tunaboats, except for nine weights for *S. attenuata* (two fetuses, two neonates, and four adults) obtained from George A. Sacher (Argonne National Laboratory, Argonne, Ill., pers. commun.).

Testes were weighed with the epididymes attached.

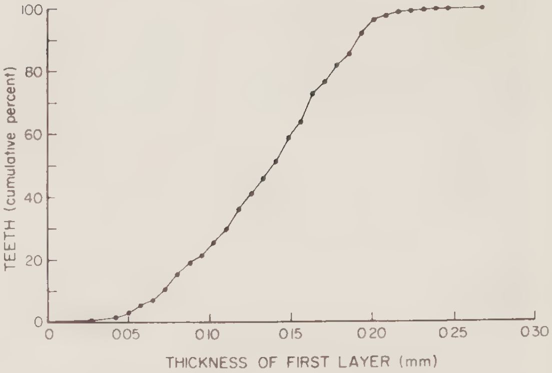

FIGURE 4.—Cumulative percent of first growth layers in relation to thickness of layer in the teeth of 417 eastern spinner dolphins showing asymptote of sigmoid curve at about 0.20 mm.

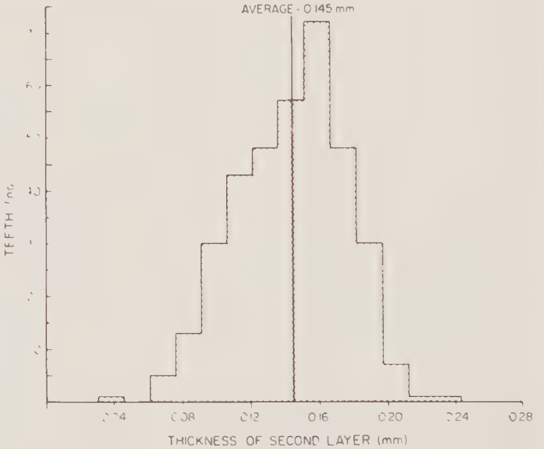

FIGURE 5.—Frequency distribution of thickness of second growth layer in teeth of 361 eastern spinner dolphins.

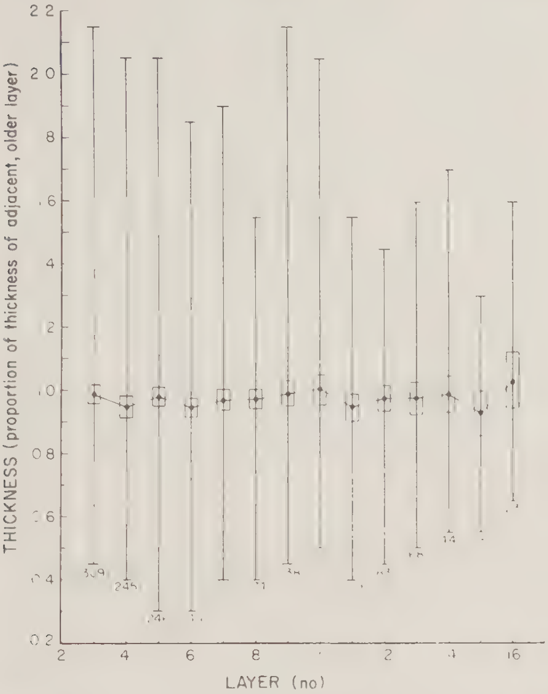

FIGURE 6.—Thickness of growth layers, beyond second postnatal layer, in teeth of the eastern spinner dolphin as proportion of thickness of next older, adjacent zone. Box is one SD on each side of mean; vertical line is range; sample size in parentheses.

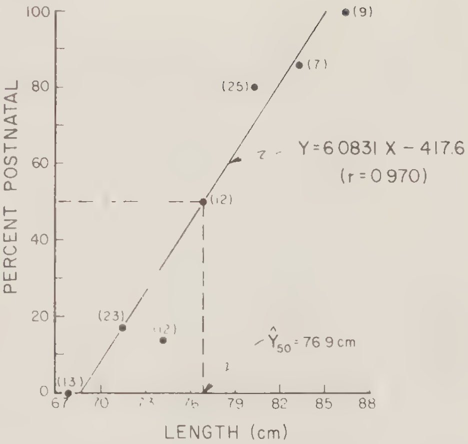

FIGURE 7.—Estimation of average length at birth, based on weighted linear regression of percent postnatal on body length, in 3-cm increments, for 101 specimens of *Stenella longirostris* (54 fetuses and 47 neonates) between 67 and 88 cm long.

RESULTS

Growth

Length at Birth

The largest fetus encountered was 84 cm long. The smallest free-swimming calf was 70 cm long. Estimated average length at birth is 76.9 cm. The estimate is based on a weighted linear regression of percent postnatal on body length, for 3-cm groupings, of 101 specimens (54 fetuses and 47 neonates) between 67 and 99 cm long (Figure 7) collected in random samples. Because of the small sizes of the available samples, 23 specimens of the whitebelly form (11 neonates and 12 fetuses) and 23 specimens unidentified to geographical form (16 neonates and 7 fetuses) were included. This is justified because of the small difference in length of adults of the two forms (<5 cm—Perrin 1975a). Such a difference could be expected to translate into a probable error in the estimate of length at birth, based on the present sample composition, of <0.5 cm, less than that to be expected to be introduced by reduction of the sample size (by 47%) through restriction to specimens known to be eastern spinner dolphins. The estimate is rounded off to 77 cm in analyses below.

This method of estimating average length at birth assumes that pregnant females and calves are 1) equally vulnerable to capture in the purse seine, 2) equally likely to die once captured, and 3) equally represented in the sample of dead animals measured. It also assumes equal rates of prenatal and postnatal natural mortality and assumes that the stresses imposed by pursuit and capture do not cause premature births during the chase or in the net. It was not possible to test these assumptions although some evidence indicates that the last may not be justified (see discussion below in The Calving Cycle and Pregnancy Rate).

Length of Gestation and Fetal Growth

The usual method used to estimate length of gestation is that of Laws (1959), in which progression of a mode in fetal lengths is followed through the seasons. This method was used to estimate length of gestation for the spotted dolphin (Perrin et al. 1976). The method could not be applied to the present samples of data for the eastern spinner dolphin, however. Although breeding is perhaps synchronous at some level (e.g., note peaks in the length–frequency distributions for postnatal males and females in February and April 1973, and February 1974—Figures 2, 3), progression of

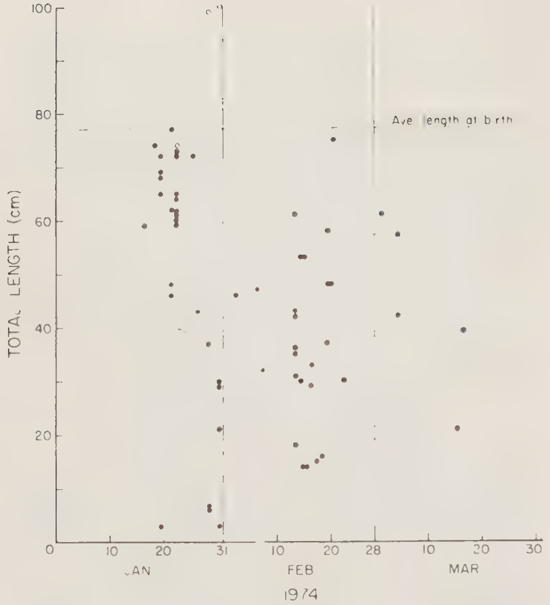

FIGURE 8.—Scatterplot of lengths of fetuses and neonates (open dots) of the eastern spinner dolphin on day of capture, January-March 1974.

fetal modes is not apparent in the data. For example, in the large samples of fetuses collected in January–March 1974 (Figure 8), a sharp mode at 60 to 75 cm in January is not apparent in February, even as neonates, and the diffuse mode at 30 to 60 cm in February is not accounted for in the January sample. A probable reason for these discrepancies is the existence of area-related differences in the timing of calving peaks or in the degree of synchrony of breeding. The tuna fleet, our source of samples, moves around from month to month. The January 1974 samples came for the most part from more easterly, offshore localities than did the February samples (Figure 9). In other words, in 1974, calving in the more offshore region may have been sharply synchronized, with a peak in February–March, while in the more onshore region, calving may have been spread over most of the year. This hypothesis is reinforced by the data for January–April 1975, when sizeable samples of fetuses were collected in the more onshore region during both January and February and smaller samples through April (Figure 10) were from more offshore (around Clipperton Island), northerly

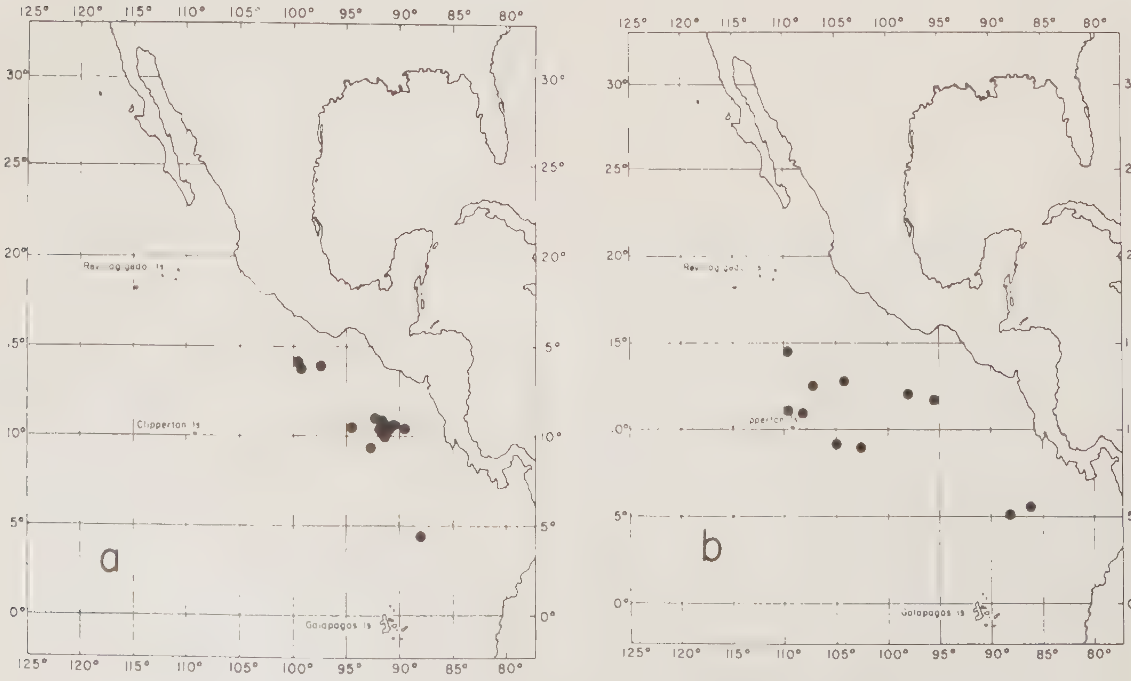

FIGURE 9.—Localities at which fetuses of the eastern spinner dolphin were collected in January (a) and February (b) 1974.

(Revillagigedos Islands), or southerly (near the Equator, east of the Galapagos Islands) regions. Even if only onshore samples are considered (those circled in Figure 10), there is no clear pattern of progression of fetal length modes (Figure 11). It is, of course, possible that the size of the population unit within which breeding is synchronous may be smaller than suggested by the onshore-offshore comparison. In any case, this complexity makes impossible the use of Laws' method for estimating gestation based on aggregated samples, and stratification of the data to even smaller areas than used above yields samples too small for meaningful analysis. For these reasons, we attempted to estimate length of gestation by two other, less direct methods: a) on the basis of relative length at birth compared with that of other, closely related delphinids for which estimates of gestation period exist, and b) on the basis of a recently discovered empirical relationship between brain size parameters and gestation in mammals.

ESTIMATE FROM COMPARISON WITH OTHER DELPHINIDS BASED ON LENGTH AT BIRTH.—Estimates of length of gestation derived by comparable methods are available for four delphinids, sensu stricto (Table 2). There is a positive correlation among these closely related forms between length of gestation and length at birth (Figure 12). Extrapolation of this relationship to

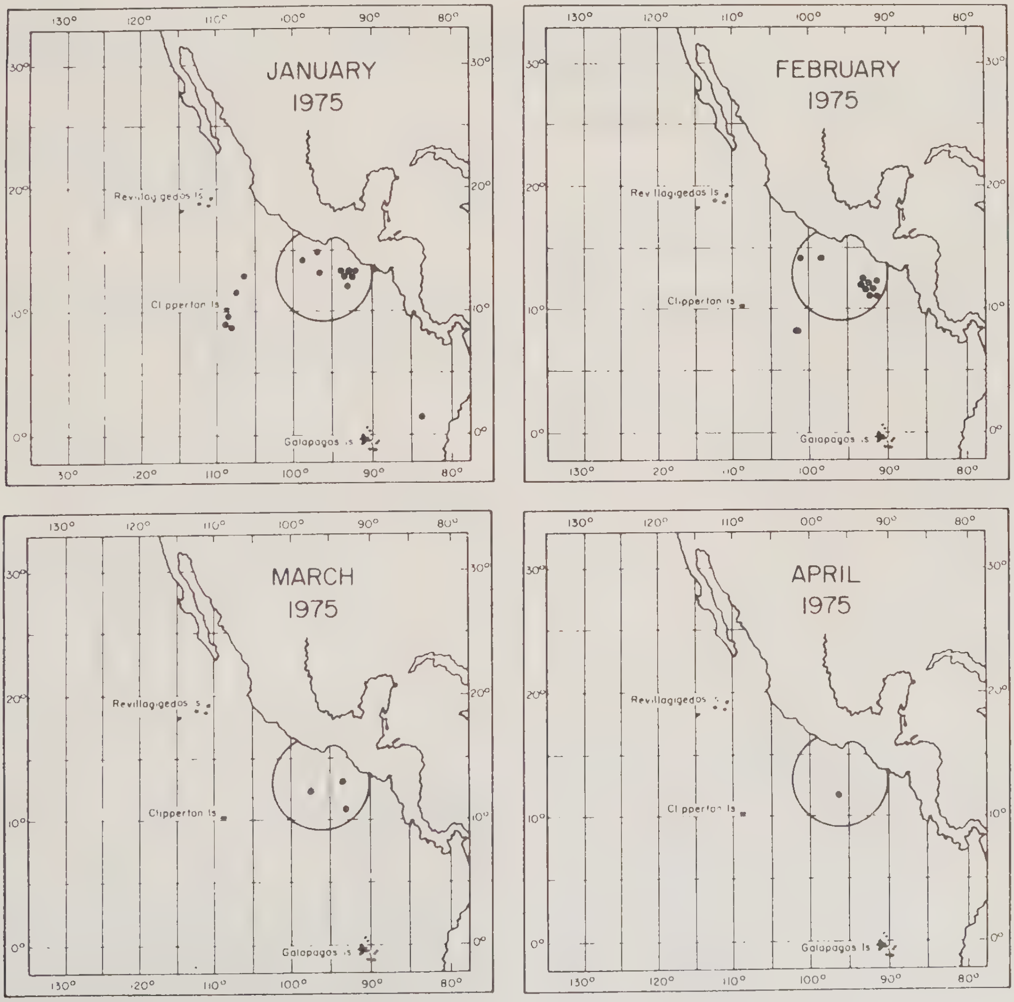

FIGURE 10.—Localities at which fetuses of the eastern spinner dolphin were collected, January-April 1975.

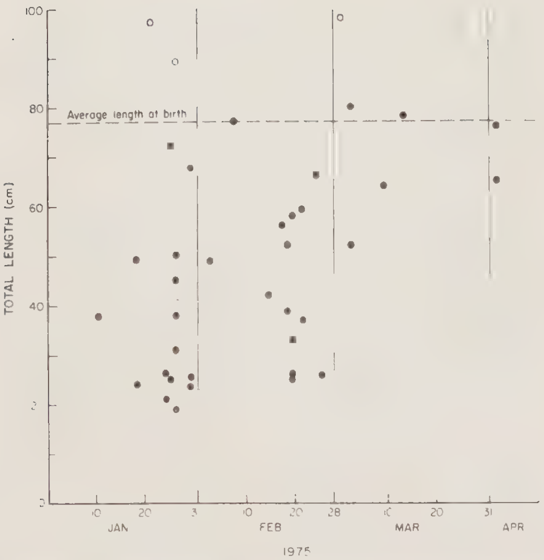

FIGURE 11.—Scatterplot of lengths of fetuses and neonates (open dots) of the eastern spinner dolphin on day of capture, January-April 1975 (specimens from localities circled in Figure 10).

TABLE 2.—Estimated average length at birth and length of gestation in four delphinids. Data for *Globicephala* from Sergeant (1962), for *Tursiops* from Sergeant et al. (1973), for *Stenella coeruleoalba* from Kasuya (1972), for *S. attenuata* from Kasuya et al. (1974) (off Japan) and from Perrin et al. (1976) (eastern Pacific). Common and scientific names follow Subcommittee on Small Cetaceans, Scientific Committee, IWC (Anonymous 1975).

Species	Length at birth (cm)	Gestation (mo)
Long-finned pilot whale *Globicephala melaena* (Newfoundland)	176.0 (average of males and females)	15.75 (15.5-16.0)
Bottlenose dolphin *Tursiops truncatus* (northeast Florida)	100.0	12.0
Striped dolphin *Stenella coeruleoalba* (off Japan)	99.8	12.0
Spotted dolphin *Stenella attenuata*		
a. (off Japan)	89.0	11.2
b. (eastern Pacific)	82.5	11.5

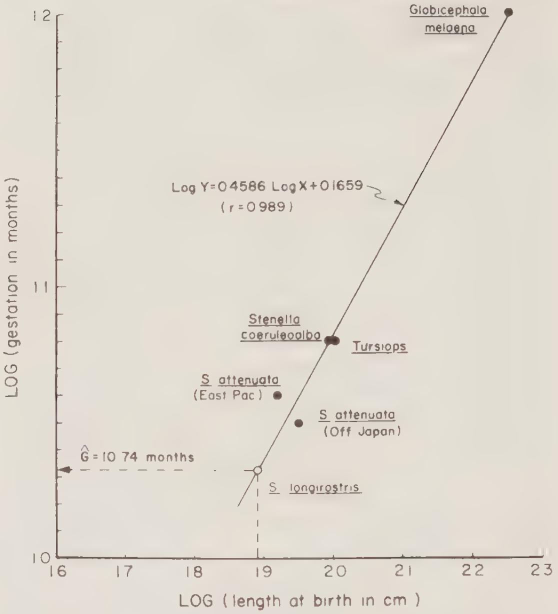

FIGURE 12.—Relationship between log of length of gestation and log of length at birth in four delphinid cetaceans, with extrapolation to predicted length of gestation in the eastern spinner dolphin.

length at birth for *S. longirostris* of 77 cm yields a deduced length of gestation of 10.74 mo (325 days).

ESTIMATE BASED ON GROWTH PARAMETERS OF THE BRAIN.—Sacher and Staffeldt (1974) recently demonstrated an empirical relationship between gestation time and brain weight in placental mammals. This relationship explains more of the wide variation in mammalian gestation times than do previous empirical approaches involving body size parameters, such as cube root of weight at birth (Huggett and Widdas 1951) or length at birth (as in above estimate). They developed a predictive equation based on linear multiple regression analysis:

$$\log G = 0.274 \log E_n + 0.144 \log A_e + 0.173 \log N + 1.853$$

where G = gestation time in days
E_n = neonatal brain weight in grams
A_e = "brain size advancement," or ratio of neonatal to adult brain weight
N = litter size (1 in cetaceans).

Application of this equation to brain data for *S. longirostris* (Figure 13—neonatal brain weight = 231 g, adult brain weight = 465 g) yields an estimate of gestation time of 286 days (9.45 mo). The method has not yet been tested on a significant number of delphinid species for which gestation time has been more directly estimated,[7] and we

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[7] The estimates used by Sacher and Staffeldt of brain weight at birth and adulthood for *Tursiops* are from Lilly (1967) and are based on samples of unstated and probably small size, a very important consideration in light of the large individual variation in these features (Figures 15, 16) and geographical variation in overall size (Anonymous 1975). For example, eight *Tursiops* brain weights summarized by Gihr and Pilleri (1969) averaged

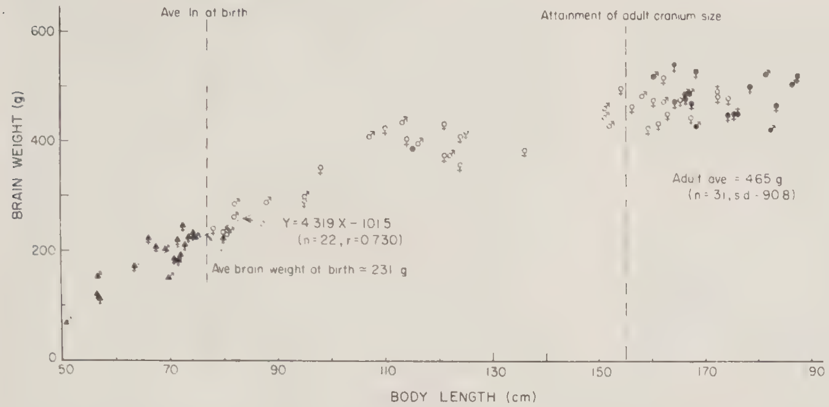

FIGURE 13.—Scatterplot of brain weight on body length for 77 specimens of *Stenella longirostris* from the eastern Pacific. The sample of fetuses and neonates (<100 cm) includes 11 eastern spinner dolphins, 9 whitebelly spinner dolphins, and 9 specimens (mostly fetuses) unidentified to race. Triangles are fetuses, open circles are sexually immature postnatal specimens, shaded circles are sexually adult specimens (by criteria explained in text below). Length at attainment of adult cranium size based on data in Perrin (1975b). The linear regression to estimate brain weight at birth is based on 22 near-term fetuses and neonates 63 to 88 cm long.

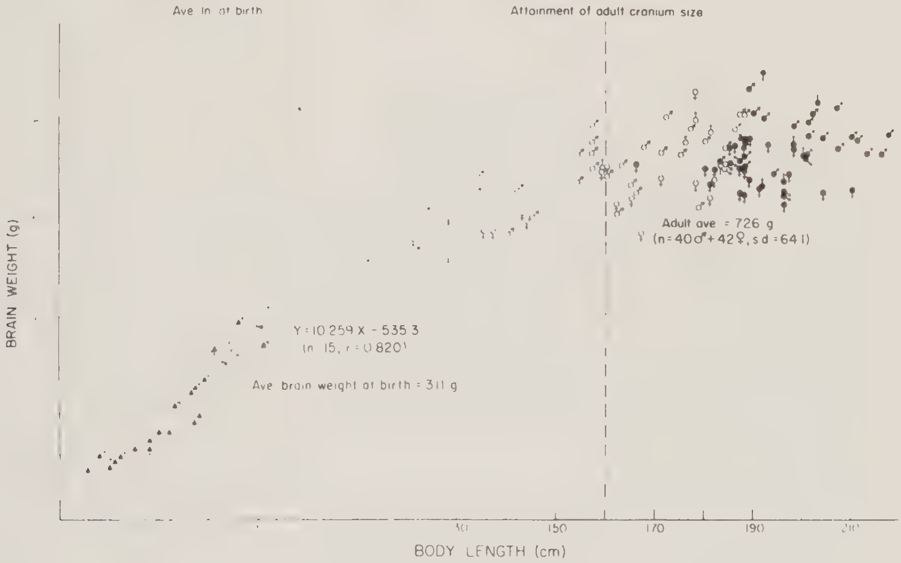

FIGURE 14.—Scatterplot of brain weight on body length for 133 eastern spinner dolphins from the offshore eastern tropical Pacific. Triangles are fetuses, open circles are sexually adult specimens. Linear regression to estimate brain weight at birth based on near-term fetuses and neonates, 73 to 91 cm long. Criteria for sexual maturity and basis for length at attainment of adult cranium size from Perrin (1975b).

1,475 g, compared with the 1,600 g reported by Lilly based on an unknown sample size. Twelve nonneonatal brain weights (probably including some of juveniles) published by Morgane and Jacobs (1972) ranged from 1,260 to 1,950 g and averaged 1,536 g. Thus, deviation of the estimate of Sacher and Staffeldt for *Tursiops* (396 days, or 13.08 mo) from the more directly obtained estimate of 12 mo (Sergeant et al. 1973), an overestimate of about 10%, is of unknown significance and probably reflects statistical error as well as possibly deductive error.

therefore applied the equation to brain data for the spotted dolphin, *S. attenuata* (Figure 14—neonatal brain weight = 311 g, adult brain weight = 726 g). The estimate of gestation time obtained is 304 days, or 10.03 mo, as compared with 11.5 mo (rounded off) estimated by a more direct method

(Perrin et al. 1976). If it be assumed that some factor in delphinid growth is unaccounted for in the Sacher-Staffeldt model and that gestation time for *S. longirostris* is underestimated to a similar degree (11.5 mo minus 10.0 mo/11.5 mo, or 13%), an adjusted Sacher-Staffeldt estimate of 10.54 mo is obtained.

The estimate based on length at birth (10.74 mo) and the adjusted Sacher-Staffeldt estimate (10.54 mo) are close to each other, and a rounded off average of the two estimates, 10.6 mo, is used below in the analyses of reproduction. Making the assumption that fetal growth follows a pattern similar to that in *S. attenuata*, i.e., that t_0 in Laws' fetal growth equation $L = a(t - t_0)$ is approximately the same proportion of gestation time as in *S. attenuata*, or 0.135 t_g (Perrin et al. 1976), a fetal growth curve can be estimated (Figure 15). The slope of the linear portion of the curve is 8.367 cm/mo, as compared with 8.283 cm/mo estimated for *S. attenuata* (Perrin et al. 1976).

Postnatal Growth

We found it impossible to estimate postnatal growth rates by the usual method of following the seasonal progression of length modes, for the reasons discussed above. We deduced an estimate of growth rate during the first 10 to 11 mo by application of the equation, $\log Y = 0.99 \log X - 1.33$, expressing an inferred relationship in toothed cetaceans between length at birth (X above) and the difference (Y above) between the growth rates during the linear phases of fetal and early postnatal growth (Perrin et al. 1976). The predicted difference based on length at birth of 77 cm is 3.60 cm/mo. Subtraction of this from the fetal linear growth (estimated above) of 8.37 cm/mo yields an estimate of average growth rate during the first 10 to 11 mo after birth of 4.77 cm/mo. If this is taken as an estimate of average growth rate during the first year, predicted length at 1 yr is 134 cm. This method overestimates length at 1 yr to some unknown, but slight extent, as growth is only approximately linear in the first year.

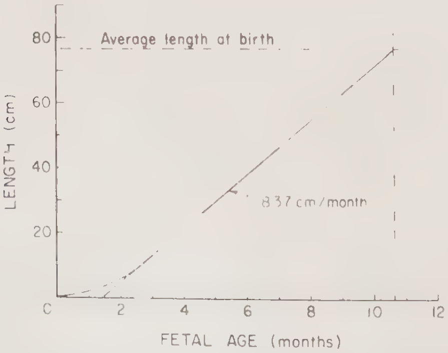

FIGURE 15.—Estimated fetal growth curve for the eastern spinner dolphin.

We examined the relationship between length and number of postnatal dentinal growth layers in the teeth for 183 males and 250 females (Figure 16). The occurrence in the samples of length-layer data for relatively more females than males with more than about 12 layers is accounted for by the fact that the sample of males selected for tooth-sectioning was stratified entirely by length, whereas the sample of females was stratified by length in juveniles and by number of ovarian corpora in adults. All females with more than 10 ovarian corpora were included in the sample, in addition to randomly selected, corpora-stratified subsamples of females with <10 corpora.

We fit growth curves to the data (to single-layer incremental means), using a two-cycle version of the Laird growth model (see Perrin et al. 1976 for discussion of the model). Juvenile males and females were considered jointly. The fit was forced through the origin (zero growth layers, and estimated length at birth of 77 cm), and asymptotic length (L_∞) was estimated as the average length of animals with 13 or more layers (L_∞ for 12 males = 179.46 cm and for 60 females = 170.91 cm), fixing the upper ends of the two curves of the second cycle. The simultaneous iterative fitting procedure arrived at 4.111 growth layers (rounded off to 4 below) as the age at which convergence of the three curves (estimated onset of a secondary growth spurt) yields the best fit (Figure 16). Estimated length at this age is 156.85 cm. The Laird/Gompertz model (Laird 1969) is

$$L(t) = L_0 \exp\left\{\frac{a}{\alpha}\left[1 - \exp(-\alpha t)\right]\right\}$$

where L = length in centimeters
t = age
L_0 = length at age zero
a = specific rate of exponential growth
α = rate of decay of exponential growth.

A form of the model generalized to the present case of more than one cycle is

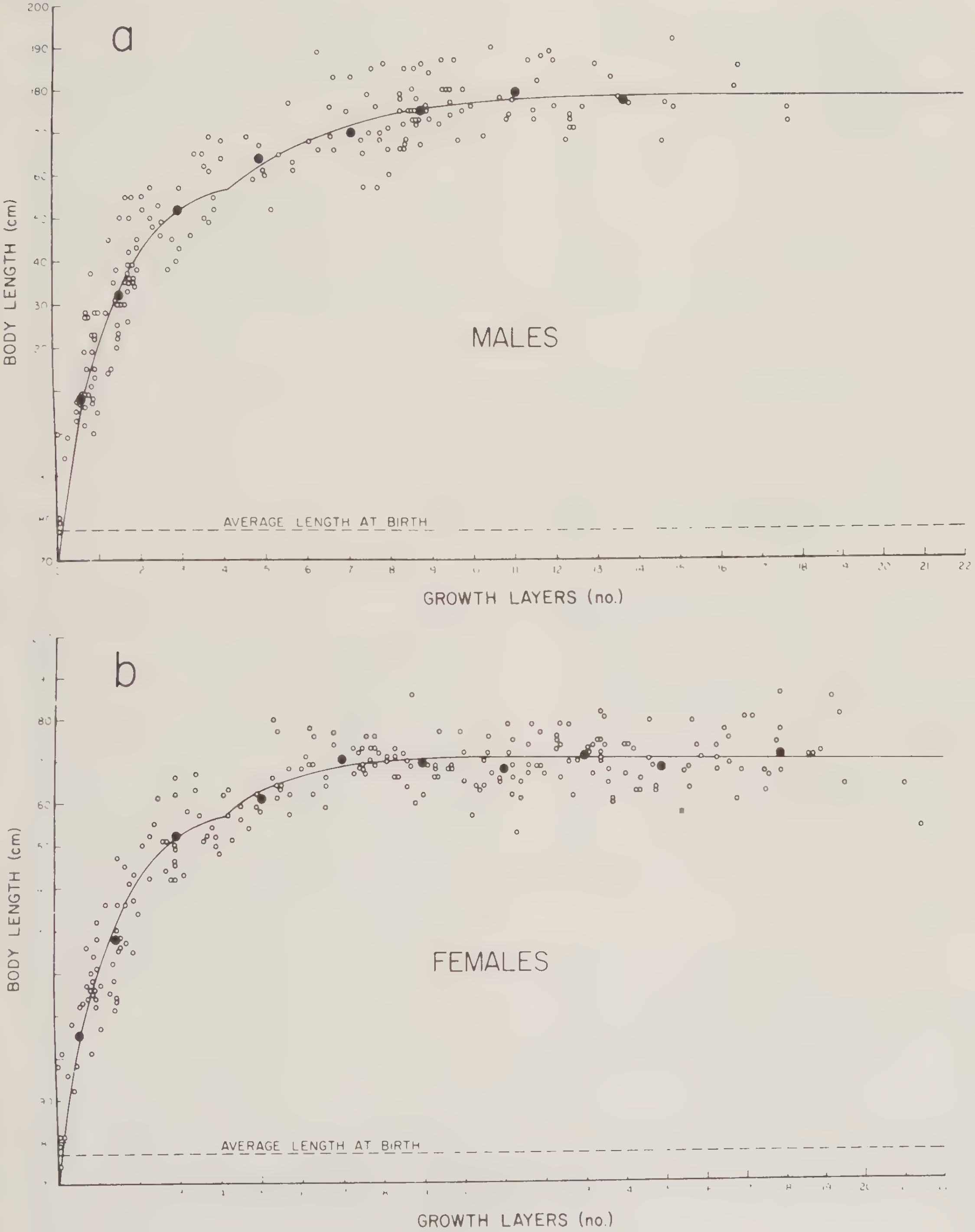

FIGURE 16.—Scatterplot of body length on number of postnatal dentinal growth layers in 183 male (a) and 250 female (b) eastern spinner dolphins. Circled dots are means for 0-1 layer, 1-2 layers, for 2-layer increments thereafter until 12 layers in males and 16 in females and for ≥12 layers and ≥16 layers, respectively. The line is a two-cycle Laird fit to single-layer incremental means (see text).

$$L(t) = L'\exp\left\{\frac{a}{\alpha}\left[1-\exp(-\alpha(t-t'))\right]\right\}$$

where L' = length (centimeters) at start of cycle

t' = age (growth layers) at start of cycle.

The growth equation for juveniles of <4 growth layers is

$$L = 77\exp\left\{\frac{0.6630}{0.9098}\left[1-\exp(-0.9098t)\right]\right\}.$$

The growth equation for males of >4 growth layers is

$$L = 156.85\exp\left\{\frac{0.0507}{0.3765}\left[1-\exp(-0.3765(t-4.11))\right]\right\},$$

and for females

$$L = 156.85\exp\left\{\frac{0.0546}{0.6354}\left[1-\exp(-0.6354(t-4.11))\right]\right\}.$$

The fits of the model to both males and females is excellent, albeit slightly better for the females about the point of convergence of the two curves than for males.

The equations rearranged and reduced for estimating age from length are

♂ and ♀ < 157 cm

$$t = -1.099\ln(6.960 - 1.372\ln L)$$

♂ > 157 cm

$$t = 4.113 - 2.656\ln(38.540 - 7.426\ln L)$$

♀ > 157 cm

$$t = 4.113 - 1.574\ln(59.871 - 11.645\ln L).$$

Note: These equations should not be used to estimate age from actual length data except for grouped samples of smaller animals (about 165 cm or less in females and 170 cm in males), for which growth rate is still large compared with individual variation in length.

Estimated age in growth layers at 134 cm, the predicted length at 1 yr derived above from extrapolative comparison with other delphinids, is 1.57 layers. Since, as discussed above, the estimate of 134 cm is likely to be a slight overestimate due to some nonlinearity of growth during the first year, the estimate of 1.57 layers is rounded down (to the nearest half layer) to 1.5 layers for use below in the various hypotheses of rate of accumulation of layers.

It appears that, effectively, in terms of the data yielded by the tooth readings, 1.5 layers are laid down in the first year. One possible explanation alternative to that of actual deposition of 1.5 layers/yr is that a single layer is laid down in the first year, but that in some individuals (about half) there is a strongly developed subsidiary line within the layer that makes the single layer appear like two layers, yielding an average of 1.5 layers. This explanation seems unlikely, however, in view of the data on thickness of the first layer. The "subsidiary line" hypothesis would predict a subsidiary inflection or plateau in the cumulative percent of first layers in relation to thickness, and such is not apparent (Figure 4).

We found no correlation between thickness of the innermost growth layer and month of capture (Table 3). It is apparent from the data that the layers are formed rapidly (very few relatively thin innermost layers are seen) and probably throughout the year in the population.

With no basis for direct calibration, we provisionally use three alternative hypotheses of rate of layer deposition (similar to those put forth for the spotted dolphin, *S. attenuata*—Perrin et al. 1976) in the age-based analyses below, namely:

I. One and one-half layers per year, or

TABLE 3.—Thickness of innermost growth layer in teeth of 331 eastern spinner dolphins, with 3-12 layers, by month of capture.

		Thickness of innermost layer ÷ thickness of next youngest layer		
Month	Sample size (no.)	Average (%)	Minimum (%)	Maximum (%)
Jan.	38	90.1	65	100
Feb.	107	83.3	20	100
Mar.	42	88.3	30	100
Apr.	13	81.1	50	100
May	9	89.9	67	100
Aug.	3	98.0	94	100
Oct.	7	71.1	47	100
Nov.	26	83.6	44	100
Dec.	5	94.0	73	91

II. One and one-half layers in the first year and one per year thereafter, or
III. One and one-half layers per year until puberty (at about nine layers in males and five to six layers in females) and one per year thereafter.

There is a rapidly increasing body of evidence (Perrin et al. 1976; Best 1976) that most delphinids accumulate growth layers at the rate of 1/yr, making Hypothesis II the most likely true of the three, but some uncertainty still exists, especially for tropical forms. We therefore express the conclusions of all age-based analyses below in terms of the three hypotheses. Other, more complex hypotheses can be suggested, but these three in our view probably include the truth.

Reproduction

The Male

Spermatogenesis is histologically evident in 50% of (right) testes weighing 94 g or more (weight of epididymis included) (Figure 17). A perhaps better criterion of sexual maturity is presence of sperm in the epididymis (Figure 18). Combined testis-epididymis weight at which half the males possess "some" or "copious" sperm in the epididymis is approximately 150 g. Another epididymal criterion can be defined, namely, the testis-epididymis weight above which the proportion of males having "copious" sperm in the epididymis does not increase, in this case above 50% at about 400 g. The three testis-epididymis weight criteria of 94 g (50% spermatogenic), 150 g (50% with sperm in epididymis), and 400 g (asymptotic weight with respect to proportion with copious sperm) are considered below in relation to body length and age (in dentinal growth layers).

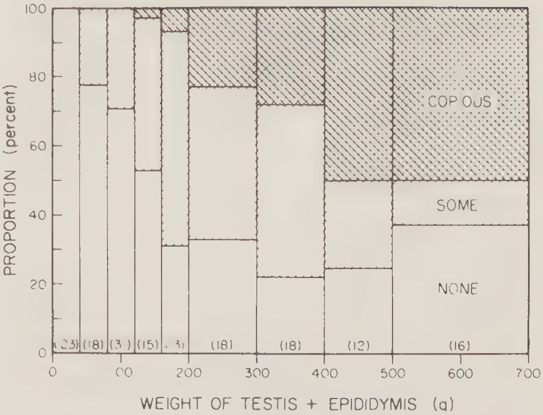

FIGURE 18.—Presence of sperm in epididymis in relation to testis-epididymis weight in the eastern spinner dolphin. Sample sizes in parentheses.

Testis-epididymis weight on the average increases precipitously with body length between 160 and 170 cm (Figure 19), but is only weakly correlated with body length beyond 175 cm. Males of any length above 160 cm can be mature or immature under each of the three criteria defined above. The proportion of males mature under the three criteria stabilizes at about 170 to 175, 175 to 180, and 180 to 185 cm body length, respectively (Figure 20). The average length of adult males under the three criteria ranges from 174 to 176 cm (Table 4).

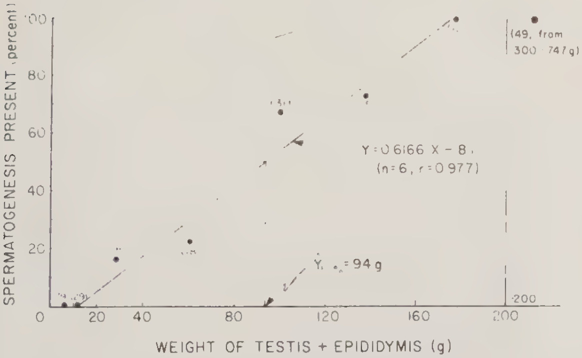

FIGURE 17.—Linear regression analysis of relationship between proportion of males spermatogenic and testis-epididymis weight in the eastern spinner dolphin. Sample sizes in parentheses.

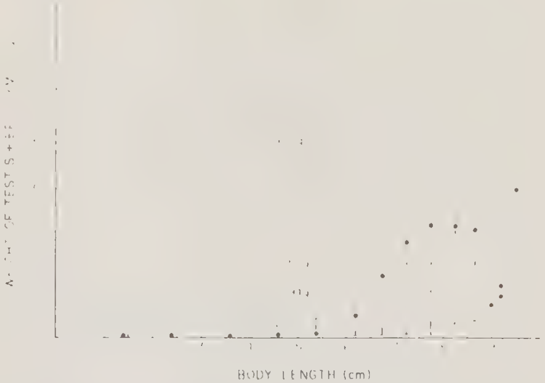

FIGURE 19.—Relationship between testis-epididymis weight and body length in the eastern spinner dolphin. Circled dots are sample means. Vertical bars are ranges. Sample sizes in parentheses.

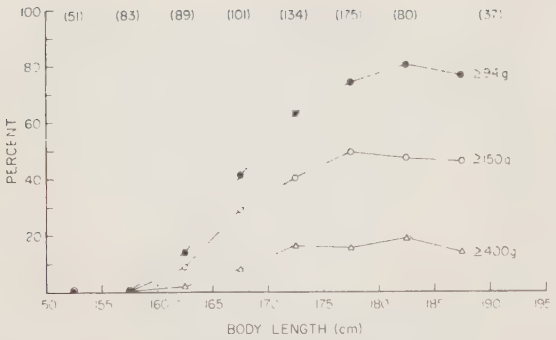

FIGURE 20.—Proportion of males sexually mature in relation to body length in the eastern spinner dolphin under three criteria of testis-epididymis weight. Sample sizes in parentheses.

TABLE 4:—Body length of adult male eastern spinner dolphins under three criteria of sexual maturity.

Weight of testis and epididymis (g)	Sample size (no.)	Body length (cm)			
		Minimum	Maximum	Average	SD
<94	594	108	192	—	—
≥94	356	160	195	176.0	5.99
≥150	230	160	195	175.8	6.06
≥400	81	162	190	174.1	5.79

Testis-epididymis weight is more closely correlated with age (in dentinal growth layers) than with body length (Figure 21). The 94-g level is reached on the average at about 9 growth layers and attained by all males with more than 12 layers. The 150-g level is reached at about 10 layers on the average and by all males at about 13 layers. The 400-g level is reached on the average at about 12 layers, but the oldest male examined (16.5 layers) had a testis-epididymis weight of only 333 g. Estimated average age in years at sexual maturity under the three criteria and under the three layer/year hypotheses ranges from 6.0 to 11.5 yr (Table 5), with the most likely estimates (Hypothesis II) 8.5 to 11.5 yr.

The question of age at attainment of social maturity (sense of Best 1969) in the spinner dolphin must await studies of social structure and breeding patterns. Other (larger) odontocetes, such as the sperm whale, *Physeter catodon*, and the long-finned pilot whale, *Globicephala melaena*, are known or thought to be polygynous, to varying degrees, but the social structure of the spinner dolphin is as yet unknown.

No systematic seasonal variation in testis weight or condition was detected, although the heavy bias in seasonal coverage of the sample precludes an adequate evaluation of this factor.

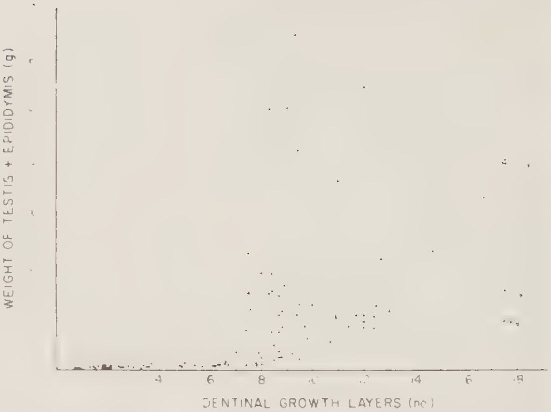

FIGURE 21.—Scatterplot of testis-epididymis weight on age (in dentinal growth layers) for 106 eastern spinner dolphins.

TABLE 5.—Estimated average age in years at attainment of sexual maturity in male eastern spinner dolphins under three criteria of maturity and three growth layer hypotheses. [See text for definition.]

Testis-epididymis criterion (g)	Age (years) under growth layer hypotheses		
	I	II	III
94	6.0	8.5	6.0
150	6.7	9.5	7.0
400	8.0	11.5	9.0

The Female

ATTAINMENT OF SEXUAL MATURITY.—The smallest sexually mature female in the present sample was 152 cm long. The largest immature female was 182 cm long. One estimate of average length at attainment of sexual maturity is the length at which 50% of the females show evidence of having ovulated, i.e. possess ovaries with one or more scars (corpus luteum or corpus albicans). This length in the present sample of eastern spinner dolphins is estimated at 164.1 cm (Figure 22).

The sigmoid curve in Figure 22 is slightly asymmetrical, that is to say, there are more immature animals (91) above the 50%-mature length of 164.1 cm than there are mature animals below it (62). At 165 cm, the numbers are 80 and 77, respectively. This length, 165 cm, is used below to classify as sexually mature or immature specimens for which ovarian data are lacking. The predicted number of growth zones (from the growth equation) at this length is 5.5.

Average age at attainment of sexual maturity can also be estimated directly from the smaller sample of females for which teeth were sectioned ($n = 247$). This analysis (Figure 23) estimates

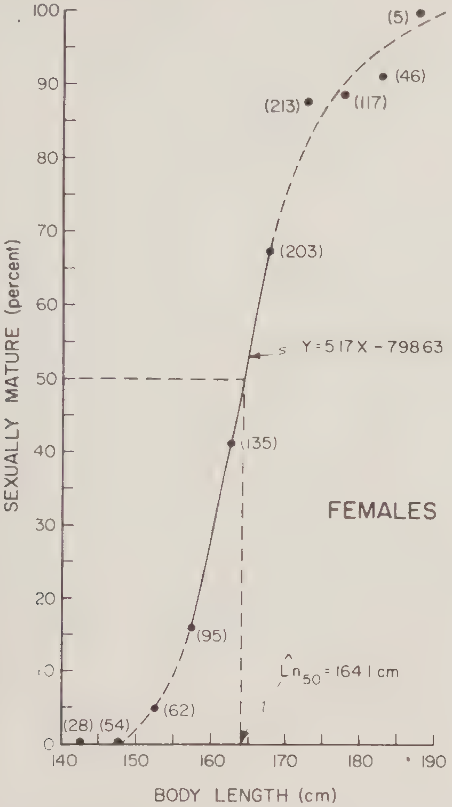

FIGURE 22.—Estimation of body length at which 50% of female eastern spinner dolphins show ovarian evidence of sexual maturity (one or more scars). Fit to central portion of curve (solid line) is linear regression. Dashed portions of curve fitted by eye. Sample sizes in parentheses.

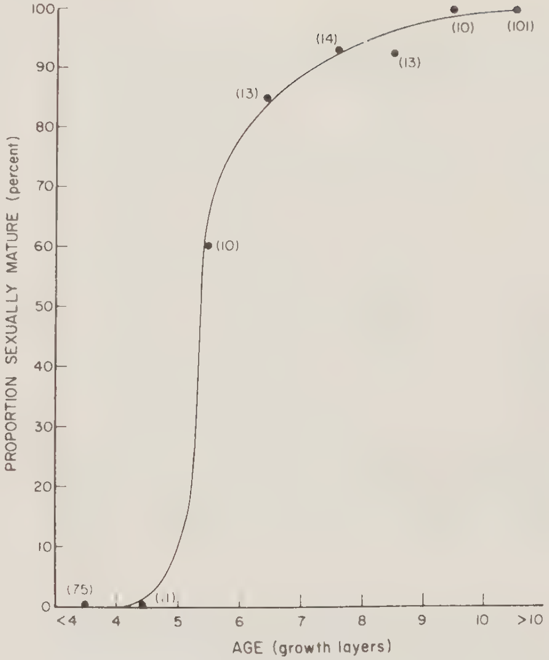

FIGURE 23.—Relationship between proportion of females sexually mature and age, in dentinal growth layers, in the eastern spinner dolphin. Fit is by eye.

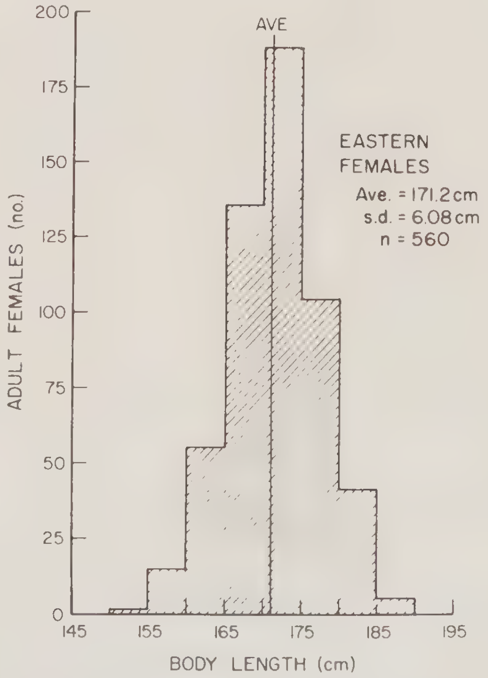

FIGURE 24.—Length-frequency distribution of 560 sexually adult (possessing at least one ovarian corpus) female eastern spinner dolphins.

average age at attainment of maturity at about 5.4 growth layers, in close agreement with the estimate derived from the age/length equation. A rounded-off average of 5.5 layers is used below. Average age in years at attainment of maturity under the three hypotheses of layer deposition rate are 3.7, 5.0, and 3.7 yr, respectively, with the second estimate being most probably correct.

Sexually adult females in the sample ranged from 152 to 187 cm and averaged 171.2 cm in length (Figure 24).

DISTRIBUTION OF CORPORA TO LEFT AND RIGHT OVARIES.—As in all other odontocetes so far studied, the left ovary predominates in ovulation. As in the case of *S. attenuata*, the distribution between left and right side (Table 6) can be accounted for by assuming that about 90 to 95% of the females ovulate the first time from the left ovary, and the remainder from the right, and that

TABLE 6.—Location of corpora (corpora lutea and corpora albicantia) in ovaries of 556 eastern spinner dolphins.

Corpora (no.)	Sample size (no.)	Location of corpora: Left ovary only (%)	Right ovary only (%)	Both ovaries (%)
1	41	92.7	7.3	—
2	51	78.4	9.8	11.8
3	50	92.0	2.0	6.0
4	43	90.7	2.3	7.0
5	56	91.1	3.6	5.3
6	53	86.8	11.3	1.9
7	60	85.0	15.0	0.0
8	39	82.1	10.3	7.6
9	26	80.8	11.5	7.7
10-11	63	73.0	19.0	8.0
12-15	55	41.8	1.8	56.4
16-19	13	23.1	0.0	76.9
20-26	6	16.7	0.0	83.3

succeeding ovulations are from the same ovary (left or right) about 90 to 95% of the time. When about 10 corpora have accumulated, emphasis shifts sharply to the opposite ovary.

OVULATION RATE.—The number of ovarian corpora, including corpora lutea, ranged from 1 to 26 in 555 sexually adult females. The frequency distribution (Figure 25) is very similar in shape to that for *S. attenuata* (Perrin et al. 1976) with highest frequencies at 5 to 7 corpora and a sharp falloff after about 10 corpora.

Size-frequency distribution of the various types of corpora albicantia among the corpora-type categories relative to total number of corpora were the same in this sample as in the sample of *S. attenuata* previously studied (Perrin et al. 1976) leading us to believe that, for this species also, corpora of ovulation persist throughout the life of the animal, accumulating at Type 3.

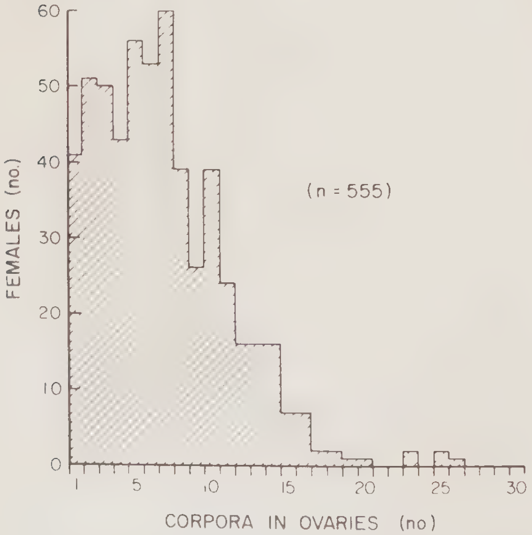

FIGURE 25.—Frequency distribution of ovarian corpora count in 555 female eastern spinner dolphins.

Scatter in a plot of number of corpora on age in growth layers is wide (Figure 26) but not as great as encountered in a study of *S. attenuata* (Perrin et al. 1976). Factors producing the scatter are 1) error in reading growth layers, 2) individual variation in ovulation rate, and 3) change in ovulation rate during the reproductive span. The teeth of *S. longirostris* in this study had more clearly defined, more easily readable growth layers than did those of *S. attenuata* in the previous study, and this probably accounts for the relatively less scatter for the former, although less influence by either or both of the other two factors cannot be ruled out.

Calculation of average ovulation rates from the data in Figure 26 must take into account individual variation in age at first ovulation. The data were grouped into 2-layer intervals (all those with 12 or more layers were included in a single final increment), and average reproductive age by interval P calculated as

$$A = \frac{\sum_{i=1}^{P} a_i b_i}{c_i}$$

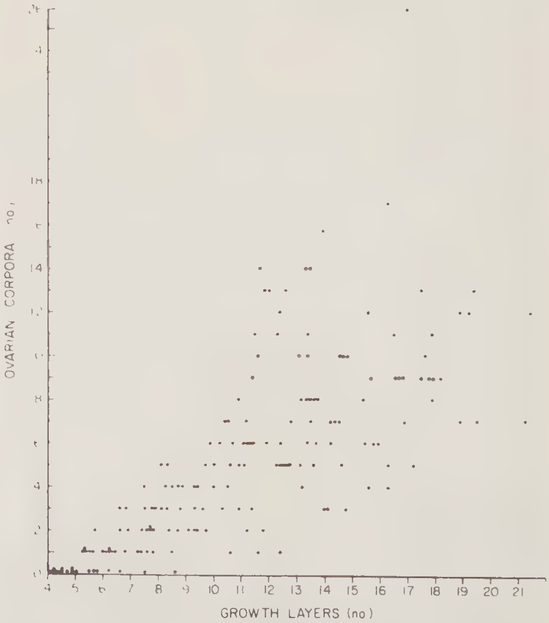

FIGURE 26.—Scatterplot of number of ovarian corpora on age, in dentinal growth layers, in 1,972 female eastern spinner dolphins.

where a_i = percent maturing in ith interval (percent maturing in i minus percent maturing in $i - 1$)

b_i = average reproductive age in interval P of females maturing in i

c_i = percent mature in interval P.

Average reproductive age in the ith interval of females maturing in i was set at 0.50 layer. A plot of number of ovulations on average reproductive age (Figure 27) shows linear increase, with a slope of unity (one ovulation per layer), in number of corpora until about 10 corpora have been accumulated at about 10 layers of reproductive age (15.5 layers total age on the average) when the ovulation rate apparently drops sharply. This is very different from the results obtained in a similar best-fit analysis for *S. attenuata* (Perrin et al. 1976), which indicated average ovulation rates of about four during the first layer, two during the second, and about one per layer thereafter. A power fit to the data for *S. longirostris* (Figure 27) shows much less variation in ovulation rate with age. It appears that in the presently sampled population of *S. longirostris* there is less multiple infertile ovulation in very young mature females than in the studied population of *S. attenuata*. This may be an inherent difference or may reflect differential status of the two populations with respect to exploitation. For example, females could on the average become sexually mature at an earlier age in an exploited population but be less fertile, in terms of pregnancies per ovulation, than had they become mature at greater age. Estimated ovulation rates were higher in the studied eastern Pacific population of *S. attenuata* than in a relatively unexploited population of the same species in Japanese waters (Perrin et at. 1976).

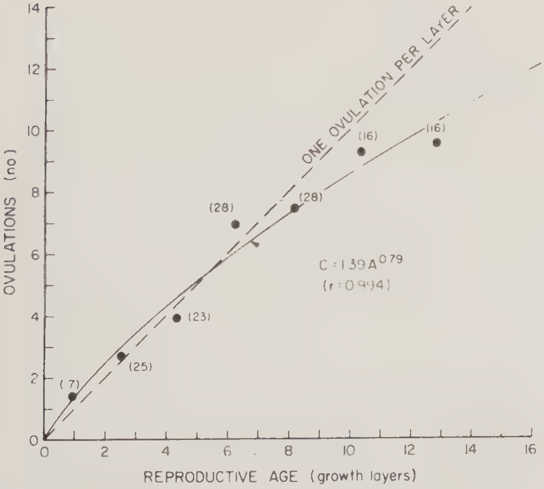

FIGURE 27.—Scatterplot of 2-layer means (last mean is for 12-16 layers) of average number of ovulations on average reproductive age in growth layers in the eastern spinner dolphin. Regression line is power fit. One-ovulation-per-layer line added. Sample sizes in parentheses.

POSTREPRODUCTIVE FEMALES.—Four adult females of 536 examined (≃1.0%) showed clear evidence of being postreproductive, or "senile," by criteria of 1) being inactive, or "resting" (neither pregnant nor lactating); 2) having high corpora count (≥10); 3) having small, withered ovaries (weighing <3.5 g); 4) having no developing follicles (largest follicle <1 mm in diameter); and 5) having no Type 1 or 2 corpora albicantia (terminology of Perrin et al. 1976), indicating recent ovarian activity (Figure 28).

THE CALVING CYCLE AND PREGNANCY RATE.—The calving cycle, for purposes of analyzing the types of field data available, can be divided into three phases: 1) pregnancy, 2) lactation, and 3) "resting"—a catch-all "phase" for animals neither pregnant nor lactating, which includes

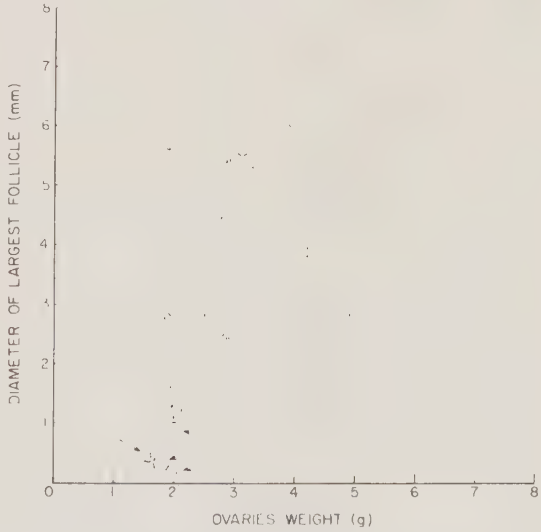

FIGURE 28.—Scatterplot of diameter of largest follicle on combined weight of ovaries for 73 adult female eastern spinner dolphins classified as "resting" (not pregnant or lactating). Specimens with corpora lutea or cystic follicles not included. Number in circle is total number of corpora in ovaries (including corpus luteum). Double circles are specimens with no Types 1 or 2 corpora albicantia indicating recent ovarian activity. Four postreproductive females indicated with arrows.

females truly resting, i.e., not ovulating because of being between cycles, those which have just ovulated but did not get pregnant, some with extremely small embryos missed in dissections, those which have recently aborted, and those which have prematurely terminated lactation due to death of the suckling calf.

The gestation phase of the cycle was estimated above, at 10.6 mo. We estimated average length of lactation by two methods; 1) by assuming that the proportion of a sample of mature females in a particular reproductive phase is directly proportional to the relative length of that phase in the overall cycle, i.e., that the samples are not biased with regard to reproductive phase (the length of the "resting" phase was also estimated this way); and 2) by assuming that a suckling calf exists for each lactating female, and the samples are unbiased with respect to suckling calves and lactating females, under which assumptions the length at which the cumulative frequency of calves in a sample equals the number of lactating females should be the average length (and, from the growth equation, age) at weaning. The first estimate was based on data for 536 adult females collected 1971–75, classified as pregnant, lactating, pregnant and lactating, "resting," or postreproductive (Table 7). The resting females were further subdivided into those with and without a corpus luteum. As discussed above, some proportion of those with a corpus luteum can be assumed to represent females not truly resting (with a corpus luteum of infertile ovulation). Only three females were simultaneously pregnant and lactating (1.44% of lactating females).

Subtraction of the postreproductive females and allocation of the females both pregnant and lactating to both of the two categories provides estimates of the proportions of the reproductive females in the three phases of the cycle (Figure 29) and of the relative lengths of the phases. Estimated average length of the phases and the total cycle can then be calculated for each 1-yr sample and for the pooled samples, using the estimated gestation period of 10.6 mo (Method 1 in Table 8). The estimates of average length of lactation thus derived range from 13.1 to 29.7 mo (the possible causes of this wide year-to-year variation in phase structure of the samples are discussed below in Gross Annual Reproduction), with a pooled average of 17.5 mo.

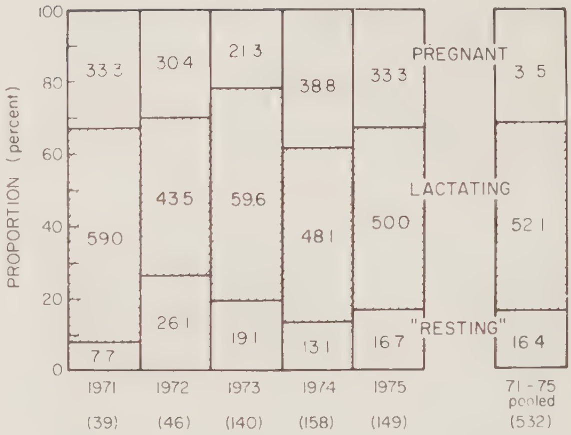

FIGURE 29.—Proportions of 532 adult reproductive female eastern spinner dolphins in pregnant, lactating, and "resting" (not pregnant or lactating) phases of cycle. Based on Table 4. Females both lactating and pregnant alloted to both phases. Postreproductive females excluded.

The second method of estimating length of lactation, the "cumulative calf length/lactating females" method yielded estimates for six single-month samples ranging from 7.7 to 16.0 mo and for single-year samples from 9.4 59 10.6 mo (Method 2 in Table 8). The pooled estimate for 1973-75 is 10.1 mo. The three yearly estimates are consistent with each other and sharply lower than the estimates yielded by the "proportion-in-phase" method above (compare in Table 9). The first method could be invalid and cause disparate estimates if 1) lactating females (and their nursing calves) were overrepresented in the samples, or conversely, 2) either (or both) pregnant or "resting" females were underrepresented. This situation could obtain if lactating females and their

TABLE 7 –Reproductive condition of 536 adult female eastern spinner dolphins collected 1971-75

	1971		1972		1973		1974		1975		1971-75 pooled	
Condition	No.	%	No.	%	No	%	No.	%	No.	%	No.	%
Pregnant only	13	33 3	14	30.4	29	20.6	60	37.3	49	32.9	165	30 8
Lactating only	23	59.0	20	43.5	83	58.9	75	46.6	74	49.7	275	51.3
Pregnant and lactating	0	0	0	0	1	0.7	2	1.2	1	0 7	4	0.7
"Resting												
with corpus luteum	0	0	4	8.7	3	2.1	5	3.1	3	2.0	15	2.8
without corpus luteum	3	7.7	8	17.4	24	17.0	16	9.9	22	14.8	73	13.6
Postreproductive	0	0	0	0	1	0.7	3	1.9	0	0	4	0.7
Total	39	100 0	46	100.0	141	100.0	161	100.0	149	100.0	536	100.0

TABLE 8.—Estimated lengths of postreproductive phases, under two methods of estimating length of lactation, of the eastern spinner dolphin based on single-year samples, 1971-75, and on pooled samples for all years, with estimates of pregnancy rate and calving interval based on lactation estimate 1.

Item	1971	1972	1973	1974	1975	Pooled
Sample size (no.)	39	46	140	158	149	532
Pregnancy (months)	10.6	10.6	10.6	10.6	10.6	10.6
Lactation (months):						
Method 1	18.8	15.2	29.7	13.1	15.9	17.5
Method 2 (Hyp. II)	—	—	10.6	9.4	10.2	10.1 (1973-75)
"Resting" (Method 1)	2.6	9.1	9.5	3.6	5.3	5.5
Sum of phases:						
Method 1						
(months)	32.0	34.9	49.8	27.4	31.8	33.6
(years)	2.66	2.91	4.15	2.28	2.65	2.80
Method 2						
(months)	—	—	26.7	25.5	26.3	26.2
(years)	—	—	2.23	2.13	2.19	2.18
Annual pregnancy rate (APR):						
Method 1	0.375	0.344	0.243	0.444	0.380	0.360
Method 2	—	—	0.450	0.474	0.459	0.461
Calving interval (1/APR):						
Method 1						
(years)	2.66	2.91	4.12	2.25	2.63	2.78
(months)	32.0	34.9	49.5	27.0	31.6	33.4
Method 2						
(years)	—	—	2.22	2.11	2.18	2.17
(months)	—	—	26.6	25.3	26.2	26.1

TABLE 9.—Estimates of length of lactation in the eastern spinner dolphin based on the "cumulative calf length/lactating females" method (see text), for 6 single-month samples and for 1973-75 by year and pooled.

Sample	Lactating females[1] (no.)	Length at which cumulative number of calves = number of lactating females (cm)	Layers	Length of lactation (months, under Hypotheses) I	II and III
Feb. 1973	41	139	1.83	14.6	16.0
Mar. 1973	18	133	1.52	12.2	12.2
Jan. 1974	23	124	1.16	9.3	9.3
Feb. 1974	42	118	0.97	7.7	7.7
Jan 1975	33	132	1.48	9.4	9.4
Feb. 1975	12	120	1.03	8.2	8.2
Year					
1973	91	128.5	1.33	10.6	10.6
1974	81	124.5	1.18	9.4	9.4
1975	88	127.0	1.27	10.2	10.2
Pooled	260	126.7	1.26	10.1	10.1

[1] Includes mature females (>165 cm) without lactation data prorated to lactating and nonlactating based on proportions in sample with lactation data

accompanying calves are more likely to be captured and killed in the net because of limitations imposed on endurance of the mother by that of the calf, certainly lower than adult endurance. The second method could yield erroneous estimates if 1) nursing calves were overrepresented in the samples, or, conversely, 2) lactating females were underrepresented. Recent data for *S. attenuata* (J. E. Powers pers. commun.) indicate that small calves are probably overrepresented in small single-set samples of that species. This may be caused by the above-mentioned lesser stamina of calves in the energetically stressful purse seine chase, capture, and release sequence. The lesser year-to-year variation in the estimates yielded by Method 2 also supports the idea that these may be better estimates. If neonates are overrepresented in the samples, however, then the percent pregnant must be underestimated to some unknown, but small, degree. In view of these considerations, both the proportion-in-phase estimate and the cumulative calf length/lactating female estimate are used below as alternatives in estimating pregnancy rate, calving interval, and gross annual reproduction, and we conclude that the true length of lactation in an unperturbed birth-to-weaning period can be assumed to lie somewhere between the estimates yielded by the two methods.

Annual pregnancy rate by Method 1 was calculated by division of the proportion pregnant (Figure 29) by the length of gestation (0.875 yr). The reciprocal of annual pregnancy rate is the estimate of average calving interval. For the Method 2 estimates, calving interval was calculated by summing the phases, taking into consideration overlapping cycles by adjusting the effective length of lactation downward by a factor equal to the percentage of lactating females also pregnant. Lacking an independent estimate of the length of the "resting" phase, the Method 1 estimate for 1973-75 was used as a reasonable approximation in the Method 2 calculations of length of cycle and calving interval.

CHANGES IN REPRODUCTIVE RATES WITH AGE.—Pregnancy rate in the sample decreases with age after about 12 layers (8.0, 11.5, or 10.2 yr, depending upon whether layer Hypothesis I, II, or III is applied, respectively), while lactation rate rises (Figure 30). Assuming that the samples are representative of the population, this may mean that 1) pregnancy rate decreases with age in the individual, or 2) that older females belong to older cohorts in which reproductive rates have been lower than in younger cohorts since recruitment to the breeding population. The former seems most likely; it would appear that older females have fewer calves and nurse them longer. The same result was obtained for *S. attenuata* in the eastern Pacific (Perrin et al. 1976).

Sex Ratios

Sex ratios are at or very near parity at birth and overall in the samples (Table 10), but there were slightly more females than males in adults in the samples for each of the 3 yr 1973-75, a result consistent with that encountered in *S. attenuata* (Perrin et al. 1976) but less pronounced.

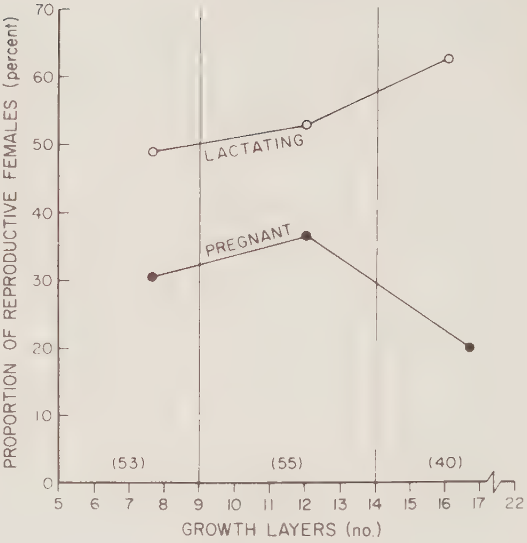

FIGURE 30.—Change in reproductive rates with age in the eastern spinner dolphin. Sample sizes in parentheses

Gross Annual Reproduction

Estimates of gross annual reproductive rates can be made based on 1973–75 samples, the 3 yr for which the samples are large and nonselected with respect to age and sex structures (Table 11). It must be noted that if, as discussed above, small calves are overrepresented in small samples (which make up most of the aggregate sample), then the proportion of total females which are reproductive and pregnancy rate (for Method 1) are underestimated and the proportion of total sample female is overestimated, all to an unknown, but probably small, degree. Standard er-

TABLE 10.—Sex ratios in 126 fetuses and 2,261 neonatal-to-adult eastern spinner dolphins. Fetal samples limited to fetuses longer than 15 cm.

Stage	Length (cm)	Sample size (no.)	Average length (cm)	Females		Males		Sex ratio (M : F)
				No.	%	No.	%	
Fetuses	>15	126	49.0	65	51.6	61	48.4	0.94
Neonates to adults	70-129	294	116.0	140	47.6	154	52.4	1.10
	130-149	269	141.2	132	49.1	137	50.9	1.04
	150-159	362	154.9	186	51.4	176	48.6	0.95
	160 (adult size)							
	1973	408	171.2	207	50.7	201	49.3	0.97
	1974	439	171.3	226	51.5	213	48.5	0.94
	1975	483	172.4	254	52.6	229	47.4	0.90
	1973-75 pooled	1,330	171.7	687	51.7	643	48.3	0.94
	Total [1]							
	1973	688	—	342	49.7	346	50.3	1.01
	1974	797	—	395	49.6	402	50.4	1.02
	1975	776	—	411	53.0	365	47.0	0.89
	1973-75 pooled	2,261	—	1,148	50.8	1,113	49.2	0.97

[1] Includes six specimens for which length data not available.

TABLE 11.—Calculation of estimates of gross annual reproductive rate of the eastern spinner dolphin, 1973-75. Standard error follows estimate (see text). Sample sizes in parentheses.

Year	*A* Proportion female	*B* Proportion of females reproductive	*C* Annual pregnancy rate		*A* × *B* × *C* Gross annual reproductive rate	
			Method 1	Method 2	Method 1	Method 2
1973	0.497 ± 0.019 (690)	0.443 ± 0.027 (343)	0.243 ± 0.036 (140)	0.450 ± 0.042 (140)	0.054 ± 0.009 (690)	0.099 ± 0.011 (690)
1974	0.496 ± 0.018 (797)	0.438 ± 0.025 (391)	0.444 ± 0.040 (158)	0.474 ± 0.042 (158)	0.096 ± 0.010 (797)	0.103 ± 0.011 (797)
1975	0.530 ± 0.018 (776)	0.432 ± 0.024 (410)	0.380 ± 0.040 (149)	0.459 ± 0.041 (149)	0.087 ± 0.010 (776)	0.105 ± 0.011 (776)
1973-75 pooled	0.508 ± 0.011 (2,262)	0.437 ± 0.015 (1,144)	0.360 ± 0.028 (447)	0.461 ± 0.024 (447)	0.080 ± 0.006 (2,262)	0.102 ± 0.006 (2,262)

rors (SE) are attached to the various estimates where sample size ≥100, under the assumption that the binomial distribution tends to normality in large samples (Bailey 1959), allowing calculation of SE as:

$$SE = \sqrt{p(1-p)/n}.$$

Although gross annual reproductive rate as calculated in Table 11 is a product of three estimates, it can be calculated directly from the total sample (number of females pregnant ÷ total number of males and females), allowing estimation of the variance by the above method. The effect on the variance by the constant used to adjust the pregnancy rate to an annual rate was ignored because the constant (11.5 mo gestation ÷ 12 mo, or 0.958) is close to unity.

The only statistically significant differences among the estimates year-to-year (at $\alpha = 0.05$) are between the Method 1 estimates for 1973 and 1974 of annual pregnancy rate and, as a result of that, gross annual reproductive rate. This sharp and real shift cannot be accounted for by a time-sampling effect, because seasonal coverage in the 2 yr was approximately the same. Prompted by the knowledge that areal variation may exist in the timing of calving peaks and/or in the degree of breeding synchrony (see Length of Gestation and Fetal Growth), we divided the data for each of the years into three geographical strata: an "inside" sample, an "outside" sample, and a "southern sample" (Figure 31). More of the 1973 sample was taken from the outside area than from the inside area (108 versus 28), and the reverse was true in 1974 (46 versus 106). The southern samples, 5 in 1973 and 14 in 1974, were too small for analysis. Comparison of the distribution of reproductive condition in inside and outside samples in 1973 and 1974, however, reveals very small areal differences compared with those between years (Table 12). It must be concluded that the sharp increase in percent pregnant and decrease in percent lactating from 1973 to 1974 is not a seasonal or areal effect. Several other possible explanations exist, to wit:

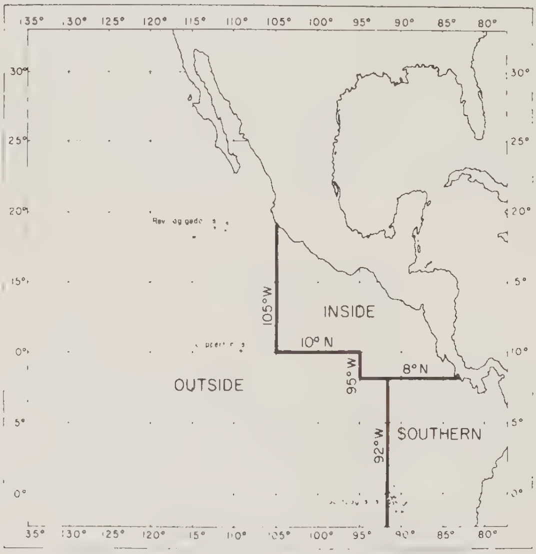

FIGURE 31.—Areas used to stratify 1973-74 samples of distribution of reproductive condition in female eastern spinner dolphins.

TABLE 12.—Distribution of reproductive condition in area-stratified samples of sexually adult female eastern spinner dolphins in 1973 and 1974.

Year	Inside (*n* = 134)	Outside (*n* = 154)
	(*n* = 28)	(*n* = 108)
1973	14.3% pregnant	19.4% pregnant
	57.1% lactating	61.1% lactating
(*n* = 136)	3.6% pregnant and lactating	0.0% pregnant and lactating
	25.0% "resting"	18.5% "resting"
	0.0% postreproductive	0.9% postreproductive
	(*n* = 106)	(*n* = 46)
1974	38.7% pregnant	39.1% pregnant
	48.1% lactating	50.0% lactating
(*n* = 152)	0.0% pregnant and lactating	4.3% pregnant and lactating
	10.4% resting	6.5% resting
	2.8% postreproductive	0.0% postreproductive

1) The samples were biased with respect to reproductive structure of the population, in one or both years or differently in the 2 yr.
2) The change was a real and normal event, perhaps reflecting differential breeding rates in single-year cohorts (the data suggest about a 3-yr cycle—see below—and the 1974 rates were similar to those for 1971).
3) An anomalous increase in pregnancy rate occurred from 1973 to 1974, perhaps related to exploitation in the tuna fishery or to natural variation in the pelagic environment.

The balance of evidence discussed above favors the first alternative, suggesting that the Method 2 estimates of gross annual reproduction are the more accurate of the two alternative sets of estimates.

DISCUSSION

Comparison with the Spotted Dolphin

The estimated gross reproductive rates (Method 1) for the eastern spinner dolphin are lower than those estimated for the offshore spotted dolphin by Perrin et al. (1976), 10 to 11%, as opposed to 14%. Three major points of difference between the data for the two species contribute to this disparity.

1) A higher proportion of the spotted dolphins were females (55.1% as opposed to 50.8% in the present 1973–75 sample of eastern spinner dolphins).
2) The proportion of total females which were reproductive was higher for the spotted dolphin (55.7% as opposed to 43.7% for the eastern spinner dolphin).
3) There is apparently much less overlapping of reproductive cycles in the eastern spinner dolphin than in the spotted dolphin in the eastern Pacific. Only 1.4% of lactating females examined were simultaneously pregnant, as opposed to 9.6% in the spotted dolphin, a sevenfold difference. At least part of this difference may be inherent in the species; the rate in the unexploited western Pacific population of spotted dolphin is 5.1% (Kasuya et al. 1974), still nearly four times greater than in the eastern spinner dolphin.

In summary, the data suggest that there is an inherent difference in reproductive capability between the spotted and spinner dolphins, but that part of the total difference in present reproductive rate may be related to differential exploitation. Gross annual reproductive rate in the unexploited western Pacific population of *S. attenuata* is estimated at 0.094 (calculated from data in Kasuya et al. 1974—0.57 female × 0.61 mature × 0.27 annual pregnancy rate = 0.094/yr), as opposed to 0.144 in the exploited eastern Pacific population of the same species, a possible example of difference in rate correlated with differential exploitation. Whereas the western Pacific population is thought to be virtually unexploited and at its original size, the eastern Pacific population is estimated to be at 62% of its original, preexploitation size (midpoint estimate).[8]

Comparison with Other Cetaceans

The estimates of gross annual reproductive rate for the eastern spinner dolphin lie at the lower end

TABLE 13.—Estimated gross annual reproductive rate of the eastern spinner dolphin compared with estimated rates for other cetaceans. Data for *S. attenuata* from Perrin et al. (1976) for eastern Pacific and Kasuya et al. (1974) for western Pacific; for *S. coeruleoalba* from Kasuya (1972), for *Delphinus* from Danilevskiy and Tyutyunnikov (1968); for *Globicephala* from Sergeant (1962); for *Delphinapterus* from Sergeant (1973); and for *Eschrichtius* from Rice and Wolman (1971). Common and scientific names follow Subcommittee on Small Cetaceans, Scientific Committee, IWC (Anonymous 1975); alternative common name in parentheses.

Species and locality	Exploited (now or in past)	Gross annual reproductive rate
Eastern spinner dolphin (porpoise), *Stenella longirostris* subsp.	Yes	0.08 (pooled 1973-75)
Spotted dolphin (porpoise), *S. attenuata*		
Eastern Pacific	Yes	0.14
Western Pacific	No	0.09
Striped dolphin (streaker porpoise), *S. coeruleoalba*, in western Pacific	Yes	0.11
Common dolphin (whitebelly porpoise), *Delphinus delphis*, in Black Sea	Yes	0.14
Long-finned pilot whale (pothead whale), *Globicephala melaena*, in western North Atlantic	Yes	0.10 to 0.13
White whale (beluga), *Delphinapterus leucas*, in western Hudson Bay	Yes	0.12
Gray whale, *Eschrichtius robustus*, in eastern North Pacific	Yes	0.13

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[8] Report of the Workshop on Stock Assessment of Porpoises Involved in the Eastern Pacific Yellowfin Tuna Fishery. SWFC Admin. Rep. LJ-76-29, Natl. Mar. Fish. Serv., NOAA, La Jolla, Calif., 109 p. (Unpubl. rep.)

of the range of estimates for other cetaceans (Table 13), with only the estimate for 1974 included in the range. The estimated rates for populations thought to have declined due to exploitation (*S. attenuata* in the eastern Pacific—Perrin et al. 1976; *D. delphis* in the Black Sea—Danilevskiy and Tyutyunnikov 1968; and *Eschrichtius*—Rice and Wolman 1971) are very close to each other, at 13 or 14%.

ACKNOWLEDGMENTS

This study would not have been possible without the generous cooperation and assistance of the owners, masters, and crews of the tuna seiners *A. K. Strom, Anna Marie, Anne M, Antonina C, Aquarius, Bernadette, Bettie M, Blue Pacific, Bold Contender, Bold Venture, Cabrillo, Captain Vincent Gann, Carol Virginia* (now *Carol S*), *City of San Diego, Commodore, Connie Jean, Conquest, Constitution, Conte Bianco, Denise Marie, Diana C, Eastern Pacific, Eileen M, Elizabeth Anne, Elsie A, Enterprise, Finisterre, Frances Ann, Gemini, Gina Karen, Independence, Jacqueline A, Jacqueline Marie, Jeanette C, Jeanine, J. M. Martinac, John F. Kennedy, Katherine Lisa, Kathleen, Kerri M, Larry Roe, Lois Seaver, Lucky Strike, Marco Polo, Margaret L., Marietta, Mary Antoinette, Mary Elizabeth, Mermaid, Missouri, Nautilus, Pacific Queen, Pan Pacific, Polaris, Proud Heritage, Queen Mary, Quo Vadis, Rosa Oliva, San Juan, Santa Rosa, Saratoga, Sea Preme, Sea Quest, Sea Royal, South Pacific, Trinidad, Venturous, Voyager, Westport,* and *Willa G.*

Scientists and technicians (in addition to two of the authors, Perrin and Holts) who collected data and specimens aboard the vessels include G. Ahern, R. E. Amick, G. M. Armstrong, S. F. Baril, A. D. Bates, R. E. Bourke, C. E. Bowlby, D. A. Bratten, R. L. Charter, J. M. Coe, R. W. Cunningham, J. D. Dohrman, R. C. Dotson, T. M. Duffy, W. E. Evans, C. M. Fedde, M. L. Fitzsimmons, W. C. Flerx, T. J. Foreman, R. K. Fountain, G. L. Friedrichsen, R. S. Garvie, J. M. Greene, J. A. Halas, D. P. Hoffman, R. Hoffmaster, R. E. Hundt, M. J. Jacobson, J. E. Jurkovich, J. LaGrange, J. F. Lambert, J. S. Leatherwood, K. P. LeVeille, R. E. Loghry, R. W. McLain, R. L. McNeely, C. W. Oliver, R. J. Olson, C. J. Orange, D. J. Otis, C. B. Peters, J. W. Ploeger, A. Poshkus, C. W. Potter, S. H. Powers, F. M. Ralston, S. B. Reiley, C. J. Ryan, O. Seth, K. D. Sexton, T. B. Shay, W. W. Steel, J. H. Thompson, P. A. Thompson, G. M. Treinen, D. Twohig, W. H. Tyndall, G. L. Ulrich, L. S. Wade, W. A. Walker, J. A. Young, D. B. Zantiny, and J. A. Zwack.

R. L. Brownell, Jr., G. D. Fitzgerald, D. W. Rice, W. A. Walker, and D. W. Waller contributed unpublished data. J. M. Coe assisted extensively with many phases of the data collection, handling and processing. J. R. Zweifel, A. L. Coan, J. E. Gilbert, T. D. Smith, and N.K. Wiley provided advice and assistance in data processing and analysis. F. G. Alverson of Living Marine Resources, Inc., provided invaluable liaison with the tuna fleet. I. Barrett, J. E. Powers, W. W. Fox, J. T. Everett, D. W. K. Au, R. L. Brownell, Jr., J. M. Coe, and D. W. Rice read the manuscript. We thank these persons and others not mentioned for their help.

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NOTES

REPRODUCTIVE PARAMETERS OF THE OFFSHORE SPOTTED DOLPHIN, A GEOGRAPHICAL FORM OF *STENELLA ATTENUATA*, IN THE EASTERN TROPICAL PACIFIC, 1973–75

Perrin et al. (1976) presented estimates of reproductive parameters of the offshore population of *Stenella attenuata* in the eastern Pacific based on data collected in 1968–73, inclusive. The sample included 3,527 specimens. Only the 1973 sample (2,036) was putatively cross-sectional with respect to age and sex structures of the kill; in earlier years, adult females were selected for examination. The purpose of this paper is to present analyses of samples collected in uniform fashion in 1973, 1974, and 1975, updating the prior report and providing a uniformly developed, albeit short, time series of annual estimates.

Methods and Materials

The data and specimens were collected by NMFS biological technicians aboard commercial tuna vessels. Data collection procedures were the same as described by Perrin et al. (1976). Data on *S. attenuata* were collected on 24 cruises in 1973, 33 in 1974, and 32 in 1975.

The total sample includes 6,243 specimens, 6,168 from precisely known localities (Figure 1). Because of the seasonal nature of the fishery, the sample is heavily biased toward the first half of the calendar year with practically no coverage of the summer months (Table 1).

Laboratory procedures were the same as reported by Perrin et al. (1976), but the analytical methods differed slightly. In calculating gross annual reproductive rate (proportion female × proportion of total females which are reproductive

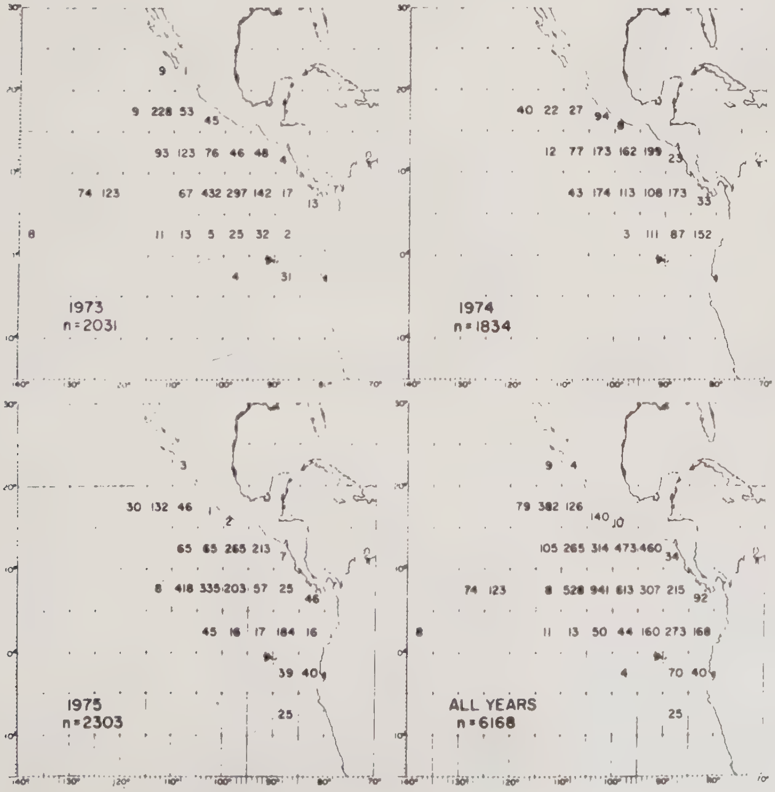

FIGURE 1.—Sample of the offshore spotted dolphin, *Stenella attenuata*, collected in 1973–75, by 5° squares.

TABLE 1.—The sample of the offshore spotted dolphin, *Stenella attenuata*, by sex, year, and month, 1973–75. Date of capture was not available for 18 of the total 6,243 specimens collected.

Month	1973		1974		1975		Total	
	♂	♀	♂	♀	♂	♀	♂	♀
Jan.	267	326	239	300	395	442	901	1,068
Feb.	200	231	428	532	249	312	877	1,075
Mar.	137	210	66	72	133	153	336	435
Apr.	41	46	35	42	135	183	211	271
May	85	156	5	2	34	35	124	193
June	56	69	36	9	30	47	122	125
July	0	0	0	0	6	12	6	12
Aug.	0	0	11	13	2	4	13	17
Sept.	0	0	1	4	0	0	1	4
Oct	5	16	0	0	31	51	36	67
Nov.	72	103	20	48	32	39	124	190
Dec.	8	9	0	0	0	0	8	9
Totals	871	1,166	841	1,022	1,047	1,278	2,759	3,466
	2,037		1,863		2,325		6,225	

× annual pregnancy rate), Perrin et al. (1976) estimated the proportion of adult females which were reproductive from coloration phase data, based on a subsample of data on percentage mature in the various coloration phases ("mottled" and "fused–adult"). In the present study, a much larger sample of complete reproductive data was available; therefore, the proportion of total females which were reproductive was estimated directly from that sample. Specimens for which ovarian data were lacking or incomplete were allocated to mature or immature categories based on a length criterion. Average length at attainment of sexual maturity was estimated as that length (177 cm) at which the number of shorter but mature specimens in the sample equals the number of longer but immature specimens.

Results and Discussion

Calving Cycle and Pregnancy Rate

The calving cycle, for purposes of analyzing field data, can be divided into three phases: 1) pregnancy, 2) lactation, and 3) "resting" (a catch-all phase for animals neither pregnant nor lactating, which includes females truly resting, i.e., not ovulating because of being between cycles, those which have just ovulated but have not become pregnant, some with extremely small embryos missed in dissection, those which recently aborted, and those which have prematurely terminated lactation due to death of the suckling calf).

We estimated the length of the cycle (and pregnancy rate) in two ways: 1) based on the reproductive structure of the sample of adult females, i.e., based on the assumption that the samples are not biased with respect to reproductive phase, and that the proportion of a sample of mature females in a particular phase is directly proportional to the relative length of that phase, using the previously estimated (Perrin et al. 1976) length of gestation (11.5 mo) as a time calibration, and 2) based on the estimate of length of gestation and a largely independent estimate of length of lactation.

The first estimate was based on data for 1,876 females classified as pregnant, lactating, pregnant and lactating, "resting," or postreproductive (Table 2). The "resting" females were further subdivided into those with and without a corpus luteum. As discussed above, some proportion of those with a corpus luteum can be assumed to represent females not truly resting (with a corpus luteum of infertile ovulation). In the total sample of 3,443 females, 61 were simultaneously pregnant and lactating (6.1% of the lactating females). Minor differences between the numbers in Table 2 and in table 8 of Perrin et al. (1976) reflect increase of the 1973 sample by eight specimens and reexamination and reevaluation of the materials.

Subtraction of the postreproductive females from the aggregate of mature females of determined reproductive condition and allocation of the females both pregnant and lactating to both

TABLE 2.—Reproductive condition of 3,469 female offshore spotted dolphins, *Stenella attenuata*, collected 1973–75.

Condition	1973		1974		1975		1973–75 pooled	
	No	%	No.	%	No.	%	No.	%
Sexually immature	522	45.0	465	45.9	580	45.7	1,567	45.5
Sexually mature								
Condition undetermined	58	5.0	60	5.9	191	15.0	309	9.0
Pregnant only	232	20.0	122	12.1	119	9.4	473	13.7
Pregnant and lactating	16	1.4	23	2.3	22	1.7	61	1.8
Lactating only	226	19.5	256	25.3	264	20.8	746	21.7
"Resting"								
With corpus luteum	34	2.9	32	3.2	28	2.2	94	2.7
Without corpus luteum	66	5.7	48	4.7	64	5.0	178	5.2
Postreproductive	7	0.6	6	0.6	2	0.2	15	0.4
Totals	1,161	100.0	1,012	100.0	1,270	100.0	3,443	100.0

categories provides estimates of the proportions of reproductive females in the three phases of the cycle and, comparing the proportions, of the relative lengths of the phases. Estimated average length of the phases and the total cycle can then be calculated for each 1-yr sample and for the pooled samples, based on the relative lengths of the phases and on the estimated gestation period of 11.5 mo (Method 1 in Table 3). The estimates of average length of cycle thus derived trend from 27.3 mo in 1973 to 42.3 mo in 1975, due to increase in the estimated length of lactation from 11.2 mo to 23.3 mo.

Annual pregnancy rate under Method 1 (also in Table 3) is calculated as proportion of reproductive females pregnant divided by the length of gestation (0.958 yr). The reciprocal of annual pregnancy rate is the estimate of average calving interval.

In the second method of calculating length of calving cycle, we estimated length of lactation by assuming that a suckling calf existed in the samples for each lactating female. Under this assumption, the length at which the cumulative frequency of calves in a sample equals the number of lactating females should be the average length at weaning (from which, using the length–age equations published by Perrin et al. (1976), the average age at weaning can be calculated). If the length of lactation increases, the average length at weaning estimated by this method should increase concomitantly. The calculated length at weaning did not increase sharply between years (Table 4). Under Hypothesis II of Perrin et al. (1976) of the rate of deposition of dentinal growth layers (two in first year and one per year thereafter—the most likely alternative), the estimated length of lactation ranges from 11.2 mo in 1973 to 12.4 mo in 1974. To arrive at estimates of the total length of the calving cycle under Method 2, we used the estimate of time spent in the "resting" phase under Method 1 for 1973 (the year for which the two estimates of length of lactation coincide exactly) or 4.6 mo, for each of the three annual estimates. This estimate is based on the assumptions under Method 1 but must suffice as a first approximation. In estimating pregnancy rate (as reciprocal of calving interval)—Table 3—overlapping cycles were taken into consideration by adjusting the effective length of lactation downward by a factor equal to the percentage of lactating females also pregnant.

TABLE 3.—Estimates of lengths of reproductive phases, pregnancy rate, and calving interval under two methods of estimating length of calving cycle (see text) of the offshore spotted dolphin, *Stenella attenuata*, 1973–75.

Item	1973	1974	1975	1973–75 pooled
Sample size (no.)	574	481	497	1,552
Pregnancy (mo)	11.5	11.5	11.5	11.5
Lactation (mo)				
Method 1	11.2	21.9	23.3	17 4
Method 2 (Hyp. II)	11.2	12.4	12.1	11.9
"Resting" (Method 1)	4.6	6.4	7.5	5.9
Sum of phases:				
Method 1				
Months	27.3	39.8	42.3	34.8
Years	2.28	3.32	3.53	2.90
Method 2				
Months	27.3	28.5	28.2	28.0
Years	2.28	2.38	2.35	2.33
Annual pregnancy rate (APR):				
Method 1	0.452	0.314	0.296	0.359
Method 2	0.472	0.459	0.461	0.463
Calving interval (1/APR):				
Method 1				
Years	2.21	3.18	3.38	2.79
Months	26.5	38.2	40.5	33.4
Method 2				
Years	2.12	2.18	2.17	2.16
Months	25.4	26.2	26.0	25 9

The 1973 estimate of length of lactation (and length of cycle, pregnancy rate, and calving interval) is very close to that obtained by Method 1 above (11.2 mo), but the two sets of estimates diverge sharply thereafter. The first method could be invalid and cause diverging estimates if 1) lactating females (and their nursing calves) were overrepresented in the samples for 1974 and 1975 or, conversely, 2) either (or both) pregnant or "resting" females were underrepresented. The first situation could obtain if lactating females and their accompanying calves are more likely to be captured and killed in the net because of limited endurance and ability to escape of the calf, certainly less than those of adults, and the strength of the mother–calf bond. The second method could yield erroneous estimates if 1) nursing calves were overrepresented in the samples or,

TABLE 4.—Estimates of length of lactation in the offshore spotted dolphin, *Stenella attenuata*, based on the cumulative calf length/lactating females method (see text) 1973–75.

			Length of lactation			
				Under hypothesis		
Sample	Lactating females[1] (no.)	Length[2] (cm)	Growth layers	I (mo)	II (mo)	III (mo)
1973	259	135.8	1.86	11.2	11.2	11.2
1974	301	138.5	2.03	12.2	12.4	12.2
1975	376	138.2	2.01	12.1	12.1	12.1
1973–75 pooled	936	137.8	1.98	11.9	11.9	11.9

[1] Includes mature females (·177 cm) without lactation data prorated to lactating and nonlactating based on proportions in sample with lactation data.

[2] Length at which cumulative number of calves number of lactating females.

conversely, 2) lactating females were underrepresented. Ongoing analyses of data for the spotted dolphin, *S. attenuata* (J. E. Powers pers. commun.), indicate that small calves are probably overrepresented in small single-set samples. In addition, the absence of sharp change in length of calves at weaning as estimated by the cumulative-calves method speaks against the alternative explanation of development between the years of differential bias against calves and lactating females. The balance of evidence favors the first alternative above, that of progressive overrepresentation of both nursing calves and lactating females as the average number of animals encircled has increased and the average number killed per net haul has decreased[1] accentuating the factor of differential stamina.

Gross Annual Reproduction

Estimates of gross annual reproductive rates can be calculated based on the two methods of estimating pregnancy rate (Table 5). It must be noted that if, as discussed above, small calves are overrepresented in small samples (which make up most of the aggregate sample), then pregnancy rate (and, therefore, gross annual reproductive rate) under Method 1 are underestimated to an unknown, but probably small, degree. This factor, of course, would also cause overestimation of the proportion of the total sample female and the proportion of total females which are reproductive, causing a countering overestimation of gross annual reproduction of unknown, but again probably small, size.

Standard errors are attached to the various estimates where sample size $\geqslant 100$, under the assumption that the binomial distribution tends to normality in large samples (Bailey 1959), allowing calculation of the standard error as:

$$SE = \sqrt{p(1 - p)/n}$$

where p = proportion (estimate of parameter)
n = sample size.

Although gross annual reproductive rate as calculated in Table 5 is a product of three estimates, it can be calculated directly from the total sample (number of females pregnant ÷ total number of males and females), to yield the same estimate and allowing estimation of the variance by the above method. The total sample size was adjusted downward by a factor equal to the proportion of mature females in unknown reproductive condition. The effect on the variance by the constant used to adjust the pregnancy rate to an annual rate was ignored, because the constant (11.5 mo gestation ÷ 12 mo, or 0.958) is close to unity.

The estimates of pregnancy rate (and gross annual reproductive rate) for 1973 and 1974 based on structure of the samples (Method 1) are significantly different from each other (using ±2 SE as an approximation of a 95% confidence interval), and the estimate for 1975, although not statistically different from that for 1974, continues the trend. The estimates based on independent esti-

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[1] Staff, Porpoise/Tuna Interaction Program, Oceanic Fisheries Resources Division. 1975. Progress of research on porpoise mortality incidental to tuna purse-seine fishing for fiscal year 1975. SWFC Admin. Rep., Natl. Mar. Fish. Serv., La Jolla, Calif., LJ-75-68, 98 p. (Unpubl. rep.)

TABLE 5.—Calculation of estimates of gross annual reproductive rate of offshore spotted dolphin, *Stenella attenuata*, for 1973–75, using two alternative estimates of pregnancy rate (see text). Standard error follows estimate (see text).

	A	B	C		A × B × C	
			Annual pregnancy rate		Gross annual reproductive rate	
Year	Proportion female	Proportion of females reproductive	Method 1	Method 2	Method 1	Method 2
1971			0.546 (86)			
1972			0.465 ± 0.023 (455)			
1973	0.572 ± 0.011 (2,037)	0.544 ± 0.015 (1,161)	0.452 ± 0.021 (574)	0.472 ± 0.021 (574)	0.141 ± 0.008 (2,036)	0.147 ± 0.008 (1,934)
1974	0.548 ± 0.012 (1,863)	0.535 ± 0.016 (1,012)	0.314 ± 0.021 (481)	0.459 ± 0.023 (481)	0.092 ± 0.007 (1,860)	0.135 ± 0.008 (1,750)
1975	0.559 ± 0.010 (2,321)	0.542 ± 0.014 (1,270)	0.296 ± 0.020 (523)	0.461 ± 0.022 (523)	0.087 ± 0.006 (2,321)	0.140 ± 0.007 (2,001)
1973–75	0.560 ± 0.006 (6,221)	0.541 ± 0.008 (3,443)	0.359 ± 0.012 (1,578)	0.463 ± 0.012 (1,578)	0.109 ± 0.004 (6,243)	0.140 ± 0.004 (5,685)

mates of lengths of gestation and lactation also trend downward, but the year-to-year differences are not statistically significant. As discussed above, the balance of evidence favors the (relatively nonvarying) estimates based on Method 2.

Although adequate data for estimating sex ratio and proportion of total females which were reproductive in 1971 and 1972, using the methods employed here, or for estimating pregnancy rate using Method 2, are not available because of selection of adult females for dissection, the estimates of pregnancy rate (using Method 1) for those two years are included in Table 5. The sample for 1971 is too small to allow direct statistical comparison with the estimates for later years, but the 1972 estimate is not significantly different from the estimates for 1973, reinforcing the suggestion that a major shift in population structure or (more likely) in degree of representativeness of the kill or the sample occurred in 1974.

In summary, the balance of evidence indicates that, in management of the dolphin/tuna situation, changes in the structure of the dolphin kill, per se, should not be taken to necessarily mean that parallel changes in reproductive rates have occurred. The changes more likely represent sampling artifacts caused by changes in the fishing and dolphin rescue operations.

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THE RIBBONFISH GENUS *DESMODEMA*, WITH THE DESCRIPTION OF A NEW SPECIES (PISCES, TRACHIPTERIDAE)

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ABSTRACT

The genus *Desmodema* is unique within the Trachipteridae in that the upper caudal lobe, borne on the second ural centrum, is not upturned, and the lower caudal lobe, borne on the first ural centrum in other trachipterids, is absent, and in that there are seven dorsal pterygiophores before the first neural spine. *Desmodema lorum* n.sp. can be distinguished from *D. polystictum* (Ogilby) on the basis of having more vertebrae, fewer caudal rays, a longer tail, and the snout longer than the eye diameter. *Desmodema polystictum* is probably circumtropical; *D. lorum* is restricted to the North Pacific Ocean. The species of *Desmodema* have a distinctive prejuvenile phase characterized by polka dots on the sides, long pelvic fins, a relatively short tail, and elongation of the first six dorsal rays. Metamorphosis is abrupt and involves loss of the pelvic fins, elongated dorsal rays and polka dots, and a great lengthening of the tail. It is suggested that metamorphosis accompanies movement to a deeper habitat. The elongated tail is related to extension of the lateral-line sensory system. On the basis of joint possession of a dermal tubercle and pore system and an abruptly constricted body, *Desmodema* and *Zu* are regarded as related. *Desmodema*, but not *Zu*, agrees with *Regalecus* in the arrangement of the dorsal pterygiophores.

The genus *Desmodema* was erected for the reception of *Trachypterus jacksoniensis polystictus* Ogilby (Walters and Fitch 1960). Fitch (1964) subsequently redescribed *Desmodema polystictum*, mainly utilizing material from the northeast Pacific, and placed *Trachypterus misakiensis* Tanaka, 1908 and *T. deltoideus* Clark, 1938 in its synonymy. Our interest arose from the observation that two recently collected specimens had what appeared to be anomalously low vertebral counts. This initiated the present study, which has revealed the existence of two species, one of them undescribed. In addition to distinguishing and describing the species, our material has allowed us to amplify the generic description of *Desmodema* and to detail some of the remarkable ontogenetic changes undergone by its species.

MATERIALS AND METHODS

Specimens used in this study are housed in the following institutions: California Academy of Sciences (CAS), Department of Biology, University of California, Los Angeles (UCLA), Natural History Museum of Los Angeles County (LACM), and Scripps Institution of Oceanography (SIO). In the material list the first length measurement is the snout-vent length (SV), the second the standard length (SL). A single value indicates snout-vent length of a broken specimen.

Because of the delicacy of the species, most of the specimens were damaged in some way, and not all counts and measurements were made on all specimens. In particular, fin lengths represent minimum measurements, since all fins seem to have been broken to some degree. No specimen appeared to have unbroken pelvic fins. Measurements are self-explanatory and were taken with flat-point dividers or dial calipers. Vertebral counts were taken from radiographs or cleared and stained material. Dorsal rays could be enumerated on only a few specimens.

RESULTS

Desmodema Walters and Fitch

Desmodema Walters and Fitch 1960. Type-species *Trachypterus jacksoniensis polystictus* Ogilby 1897, by original designation.

Diagnosis.—A trachipterid with 4-10 caudal rays, the caudal on the same axis as the caudal peduncle, all caudal rays borne on terminal centrum, no lower caudal lobe. Seven dorsal pterygiophores before first neural spine. Body con-

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Manuscript accepted March 1977.
FISHERY BULLETIN: VOL. 75, NO. 4, 1977.

stricted behind anus, tail exceedingly elongated in juveniles and adults. Young with numerous dark round spots. Skin of adults pierced by numerous pores.

Description—Body strongly compressed laterally, postanal portion of body narrowing into a whiplike tail in juveniles and adults (posterior vertebrae about four times as long as 14th vertebra). Posterior region of body of larvae and prejuveniles narrow, but not exceedingly elongate (posterior vertebrae shorter than 14th vertebra). Seven pterygiophores before first neural spine, one or two pterygiophores between first and second neural spines. First pterygiophore closely applies to back of skull, no predorsal bones. Anterior five or six dorsal rays elongated in larvae and prejuveniles to form a dorsal pennant: these rays completely lost in adults. Pelvics long and fanlike in young, absent in adults. Caudal well developed, of 4-10 unbranched rays, parallel to axis of tail. Caudal rays all borne on last ural centrum, no ventral caudal lobe (Figure 1).

Fin rays with a lateral row of small spines, these weak or absent on posterior pelvic rays, middle caudal rays, and pectoral rays. Each dorsal ray anterior to elongated tail portion of body with a single laterally directed stout spine on either side of the base.

Lateral line ending at caudal base, lateral-line scales with a pair of spines. Body otherwise scaleless at all sizes (*D. polystictum*), or young covered with scales, each with a pair of longitudinal spinous ridges (*D. lorum*). Skin of adults with cartilaginous tubercles, and pierced by numerous pores (Walters 1963). No enlarged tubercles on ventral midline.

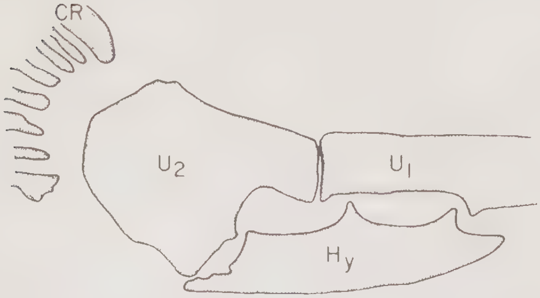

FIGURE 1.—Caudal skeleton of *Desmodema polystictum*, SIO 73-340. Camera lucida drawing at 25× magnification. Only bases of caudal rays shown. CR, caudal ray; Hy hypural; U_1, first ural centrum; U_2, second ural centrum and hypural.

Two nostrils in prejuveniles, the posterior just before anterior margin of eye; posterior opening obliterated in juveniles and adults. Nasal epithelium without ridges or folds at all sizes. Head bones cancellous and ridged. Mouth strongly oblique. Teeth restricted to one to four in each premaxilla and two enlarged, recurved fangs on mandible, one on either side of symphysis. Gill rakers (2-3) + (9-10) usually 3 + 9, fleshy, distally expanded and leaflike. Rakers of upper limb with a few teeth. Pseudobranch well developed. Gas bladder present in small juveniles (to about 30 mm SV), rudimentary or absent in large juveniles and adults.

Very young silvery, prejuveniles silvery with profuse dark spotting, adults without spots.

Growth changes.—Although we have no material smaller than 18.9 mm SV, it appears that development from a silvery or transparent form with a triangular outline with the head deepest, into the polka-dotted, deep bodied prejuvenile is gradual. The transition from prejuvenile to juvenile is probably rapid and can fairly be termed a metamorphosis. There is a large-size gap in our material of *D. polystictum* (91-260 mm SV), but our material of *D. lorum* includes the appropriate size classes. The difference between the prejuvenile and the final body form can be seen in Figure 5. The two specimens are almost identical in snout-vent length. However, the upper specimen is essentially a miniature adult. The major differences are in the change in the ventral profile, elongation of the tail, increase in eye size, eruption of lower jaw teeth, and loss of the spots, pelvic fins, and posterior nostril. Juveniles, including our largest (173 mm SV) have an elongate opening not yet covered over by the skin at the position of the pelvic fins, indicating that loss of the pelvics may be rapid, and from the base.

Walters (1963) indicated that juveniles of *D. polystictum* are scaled, but that adults are scaleless, and have cartilaginous tubercles and a subdermal canal system connected to the surface by numerous pores. In our material of *D. lorum* an 18.5-mm SV silvery individual lacks both scales and tubercles. An individual 36 mm SV is scaled, but lacks tubercles, and in another (36.5 mm SV), tubercles are present ventrally, and on the sides behind the head. Our largest polka-dotted prejuvenile is 95 mm SV. The upper sides are scaled; the remainder of the body is covered with tubercles and the subcutaneous canal system is well developed, with surface pores present. A juvenile of 104 mm SV has scales along the dorsal base, and one of 131 mm SV lacks scales and has tubercles and pores over the entire body.

Desmodema polystictum does not agree with *D. lorum* in the course of development of the tubercles and pore system. None of our specimens has scales. Instead tubercles are developed in a specimen of 36 mm SV, and tubercles and pores are present in an individual of 42 mm SV. Walters (1963) was unaware of the existence of the two species of *Desmodema* and his figure 1 was undoubtedly based on a juvenile of *D. lorum*.

In juveniles the first six dorsal rays are elongated (broken in all our specimens). These rays, which are borne on the pterygiophores before the first neural spine, are lost, and in adults represented by a stiffening in the skin. The recurved, fanglike lower jaw teeth first appear at a snout-vent length of about 100 mm.

Life history and behavior.—We lack data from closing nets, and thus have no precise information on depth of capture of our material. Fitch and Lavenberg (1968) inferred that *Desmodema "polystictum"* lives "500 to 1,000 feet beneath the sea's surface" and Walters (1963) predicated his discussion of energetics on the assumption that *Desmodema* is mesopelagic. Harrison and Palmer (1968) speculated that *Desmodema*, which they described as "chocolate brown," might live deeper than its silvery relatives. Actually *Desmodema* is silvery and turns brown in preservative.

The number of polka-dotted juveniles of *D. polystictum* taken at or near the surface indicates that they probably mainly occupy the euphotic zone. The polka-dotted pattern would be maximally useful as protective coloration in the light-dappled environment near the surface. However, records (presumably juveniles) from stomachs of *Alepisaurus* (Fourmanoir 1969) suggest a considerable depth range. A number of juvenile *D. lorum* have been taken from albacore, *Thunnus alalunga*, stomachs, and others have been taken by gear fished near the surface. We see no reason to assume that the albacore had been feeding "far beneath the surface" (Fitch 1964); however, Fitch figured a metamorphosing juvenile of *D. lorum* from an *Alepisaurus* taken on a longline and listed four other such specimens, again indicating a wide depth range. Several of the metamorphosed specimens of *D. lorum* were taken by open nets fished to considerable depths. However, three of the largest specimens were taken in purse seines, indicating depths of capture of no more than 100 m. We have three adult *D. polystictum*: two were taken in nets towed in the upper 500 m, and one was taken in a purse seine.

Fitch's (1964) report on stomach contents provides equivocal evidence; *Idiacanthus* is a mesopelagic vertical migrator, but *Phronima sedentaria* occurs in the upper 300 m (Eric Shulenberger, Scripps Institution of Oceanography, pers. commun.). There is thus no objective evidence that either species of *Desmodema* lives below 500 m (although the possibility is not excluded). The species of *Desmodema* would seem to be members of the deep epipelagic group as defined by Parin (1968).

Keeping in mind the sketchy nature of the available data on depth distribution, the following hypothetical scheme is suggested for both species. The silvery young have a gas bladder. The large fins and the deep head and rapidly tapering body suggest that they are feeble swimmers. They are probably epipelagic. The polka-dotted prejuveniles probably occupy the euphotic zone. The tail is short and anguilliform propulsive waves could involve almost the entire body. The very elongate, fanlike pelvic fins and dorsal pennant indicate that swimming is normally slow and probably involves undulations of the dorsal fin, rather than the body.

With metamorphosis the dorsal pennant and the pelvic fins are lost, the latter dropping off entirely. The tail rapidly elongates at this time (see Figure 5). The polka-dotted pattern is also lost, but more gradually. The greatly elongated tail with its associated dorsal rays would produce drag during active swimming, but probably less so than in *Trachipterus*, in which the posterior part of the body is deeper. We propose that adult *Desmodema* normally occupy the twilight zone of a few hundred meters, where they hover, probably in a head-up posture, maintaining position by undulations of the dorsal fin. Rapid bursts of anguilliform swimming would accompany prey capture or predator avoidance. The tubercle and pore system might act to maintain laminar flow during burst swimming, as hypothesized by Bone (1972) for the oilfish, *Ruvettus*.

The elongate tail of *Desmodema* can be related to the hypothesized mode of life. The lateral line runs the length of the tail, ending at the caudal. The tail then serves the function of greatly extending the lateral line, and in effect provides an antenna for the reception of water displacement and low frequency sound. In this connection it may be pointed out that in the related *Stylephorus chordatus* the lateral line is continued onto the exceedingly elongated caudal filament (R.H. Rosenblatt pers. obs.). *Stylephorus* has tubular eyes directed forward, and it is assumed that it maintains a vertical posture in the water (Marshall 1971:44). That elongate bodies in deep-sea and pelagic fishes are related to a sensory function has been suggested by Wynne-Edwards (1962:80).

Our presumption is that adult *Desmodema* hover vertically, visually seeking prey silhouetted against downwelling light. The lateral-line system of the tail would be used to sense predators approaching beneath the field of view of the eyes. Undulations of dorsal fin would be used for position-holding and the lateral body musculature used for burst swimming for prey capture and predator avoidance.

This mode of life may predominate in the elongate trachipteroids. Nishimura (1963) has inferred a similar life-style for *Trachipterus ishikawai*. Adults of *Zu cristatus* have a long, thin tail, reminiscent of that of the species of *Desmodema*, and Clarke and Haedrich (in Gaul and Clark 1968) recorded the following observation: "A large oarfish, *Regalecus glesne*, was sighted at about 210 meters. It was hanging vertically in the water, head up, and appeared to be almost two meters in length . . . . The dorsal fin was moving continuously with wave-like motions progressing from the head end to the tail end, very much like the fin motions seen in file fish."

Distribution.—Desmodema polystictum is probably circumtropical, and *D. lorum* appears to be restricted to the northern Pacific (Figure 2). The most obvious feature of the distributions is the lack of sympatry. *Desmodema polystictum* is broadly distributed in the tropical Pacific; the northern and southernmost records for the species are in areas influenced by warm currents. *Desmodema lorum* on the other hand is mostly restricted to the cooler waters of the North Pacific. Twenty of the 21 eastern Pacific specimens were taken north of lat. 28°N, that is in areas north of the 20°C August surface isotherm and the 9°C 200-m isotherm. The single western Pacific capture (a metamorphosed juvenile) was in the area where the temperature at 200 m is about 16°C.

The only area of possible sympatry indicated is near Cape San Lucas, lower California, where there are several records of *D. polystictum* and a single record of *D. lorum*. Occurrence of the latter that far south may be related to transport by the California Current.

From Figure 2 it appears that both species of *Desmodema* are especially common in the eastern Pacific. The pattern of captures more likely reflects effort. Many of the specimens of *D. polystictum* have been taken incidentally by the purse seine tuna fishery, which is concentrated in the eastern tropical Pacific. Similarly the predominantly eastern records for *D. lorum* probably reflect the intensive collection effort in the region of the California Current.

The presence of *D. polystictum* in the Atlantic rests on the records of Leapley (1953) and Walters (1963). G. Krefft, Instit für Seefischeri, Hamburg, has informed us that the RV *Walter Herwig* has taken several specimens of *Desmodema* in the central and southern Atlantic, but that the material is not available for study at the present time.

Comparison and relationships.—Walters and Fitch (1960) distinguished *Desmodema* from *Trachipterus* primarily on the basis of the nature of the caudal fin (parallel to the body axis), the length of the gastric caecum (long), the absence of sharp-tipped midventral tubercles, and the presence of scales in *Desmodema*. The last character is not diagnostic, since our study indicates that *D. polystictum* lacks scales at all sizes. The caudal structure of *Desmodema* is unique in the Trachipteridae in that all of the caudal rays are borne on the terminal centrum and the hypural of the first ural centrum is rayless (Figure 1). Additionally, in the species of *Desmodema* there are seven pterygiophores before the first neural spine and one or two between the first and second neural spines, and in *Zu* and *Trachipterus* there is a single pterygiophore before the first neural spine, and nine between the first and second neural spines.

Walters (1963) regarded *Zu* as the most generalized and *Desmodema* as the most specialized of the three trachipterid genera. Despite the specializations unique to *Desmodema* and *Zu* respectively, present evidence indicates that the two genera are more closely related to each other than either is to *Trachipterus*. The most important indicator of relationship if the presence in both of the dermal tubercles in large prejuveniles, and tubercles and a cutaneous pore system in juveniles and adults. Dermal tubercles,

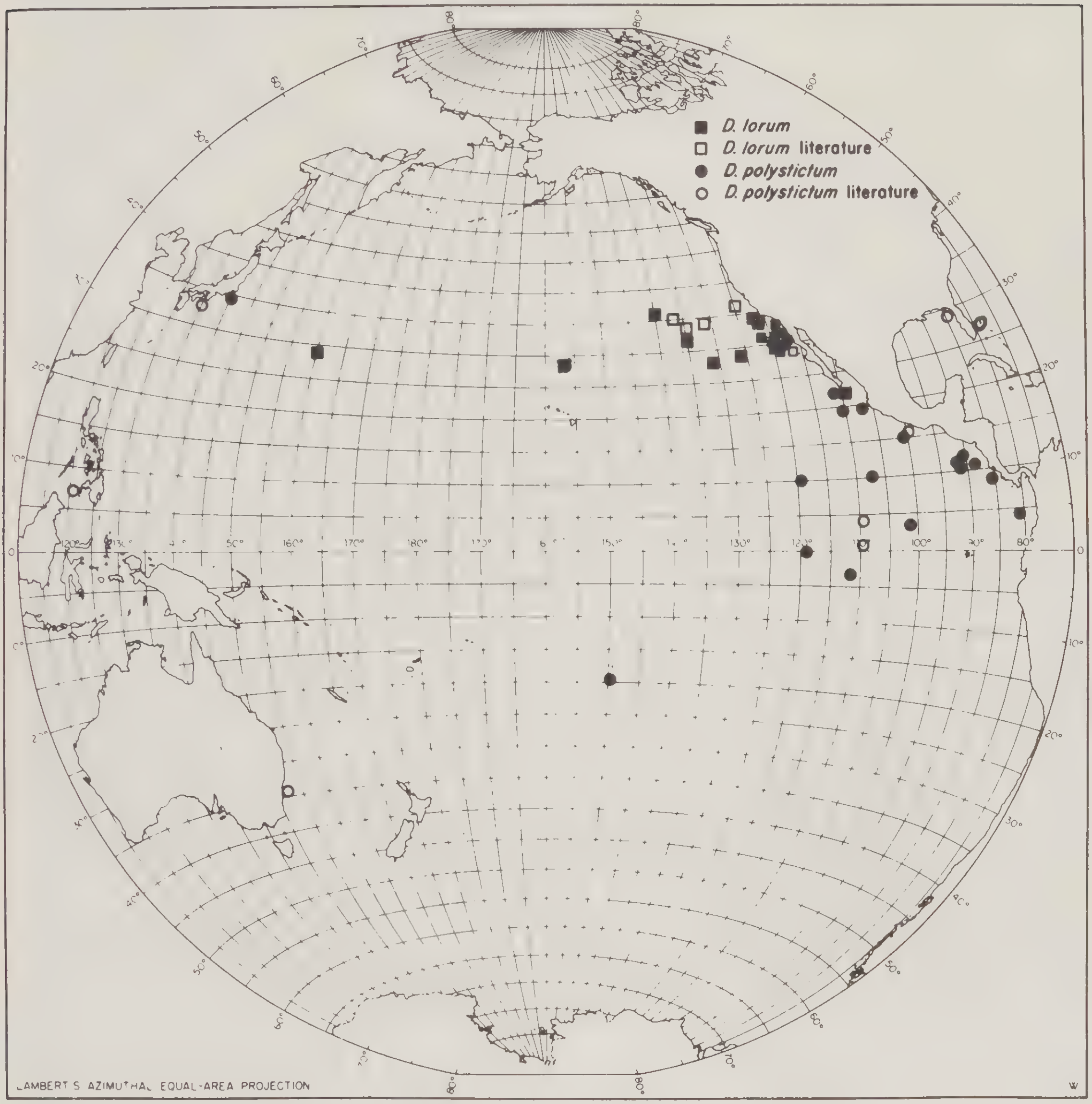
■ D. lorum
□ D. lorum literature
● D. polystictum
○ D. polystictum literature
LAMBERT'S AZIMUTHAL EQUAL-AREA PROJECTION
120°
160°
170°
180°
130°
100°
80°
0
10°
20°
30°
40°
50°
60°
70°
80°

FIGURE 2.—Distribution of the species of *Desmodema*.

pores, and subdermal canals have not previously been reported for *Zu cristatus*. Instead the species has been described as having deciduous cycloid scales (Tortonese 1958; Walters and Fitch 1960; Palmer 1961; Fitch 1964). However, none of our specimens (8, 27.5-811 mm SL) has scales. Two specimens of about 40 mm SL have the skin intact and smooth, except for small tubercles on the lower sides anteriorly, with no trace of scales. Two specimens of 135 and 141 mm SL respectively have the body studded with soft tubercles, with a few interspersed pores; in a specimen of 210 mm SL both tubercles and pores are well developed. In the 811-mm SL adult the skin is superficially very similar to that of *Desmodema*. Our 135-mm SL specimen is from the Atlantic, so it does not appear that we are dealing with a difference between Atlantic and Pacific populations. We can only surmise that the tubercles and pores of *Zu* have been taken to represent scale pockets left behind by deciduous scales. The "modified cycloid scales" mentioned by Harrisson and Palmer (1968) may have been the dermal tubercles.

In addition to the tubercle and pore system, *Zu* and *Desmodema* agree in two other specialized characters: the body is constricted behind the vent to form an elongated, slender tail, and there is a distinctive prejuvenile which metamorphoses into the juvenile phase.

In our interpretation, *Trachipterus* is the most generalized trachipterid genus, with *Desmodema* and *Zu* specialized in respect to the characters given above. *Desmodema* is advanced with respect to *Zu* in the loss of the lower caudal rays and great elongation of the tail, and probably in the crowding of the pterygiophores before the first neural spine. The significance of the difference in the relationship of the anterior dorsal fin pterygiophores between *Trachipterus* and *Zu* on the one hand and *Desmodema* on the other is difficult to interpret. In *Lophotus* there is a single rayless pterygiophore before the strongly forward-curved first neural spine, then about 15 uncrowded pterygiophores in the wide interspace between the first and second neural spines. The figure of *Regalecus* given by Parker (1886) clearly shows a condition much like that of *Desmodema*. Although the caudal of *Regalecus* has been described as lacking a ventral lobe, we find that two caudal rays are associated with the terminal centrum and four with the (ventral) hypural of the first ural centrum.

Desmodema polystictum (Ogilby)

Figures 3, 4

Trachypterus jacksoniensis polystictus Ogilby 1897:649; Newcastle, New South Wales, Australia; holotype, Australian Museum.

Trachypterus misakiensis Tanaka 1908:52, pl. IV, fig. 2, "shores of Misaki" Japan; holotype, Zool. Inst. University of Tokyo, No. 960. Herre and Herald 1951:318, fig. 3; 6°26′N, 121°35′E.

Trachypterus deltoideus Clark 1938:180; Rurutu Island, "Australs" (Tubuai Islands); holotype, CAS 5532.

Desmodema polysticta. Walters 1963:260; 28°58′N, 88°18′W; Integumentary system. Fitch 1964:230; in part, see synonymy of *D.*

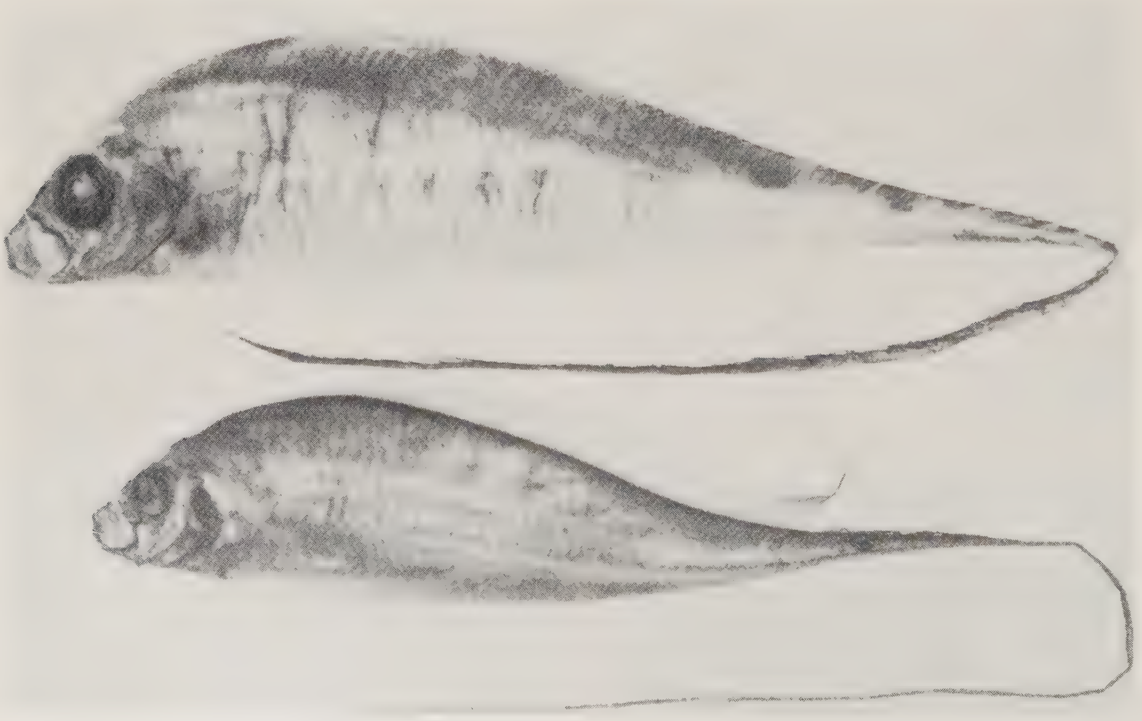

FIGURE 3.—Adults of the species of *Desmodema*. Upper figure *D. polystictum*, SIO 68-333, 1,040 mm SL. Lower figure holotype of *D. lorum*, USNM 216726, 1,098 mm SL.

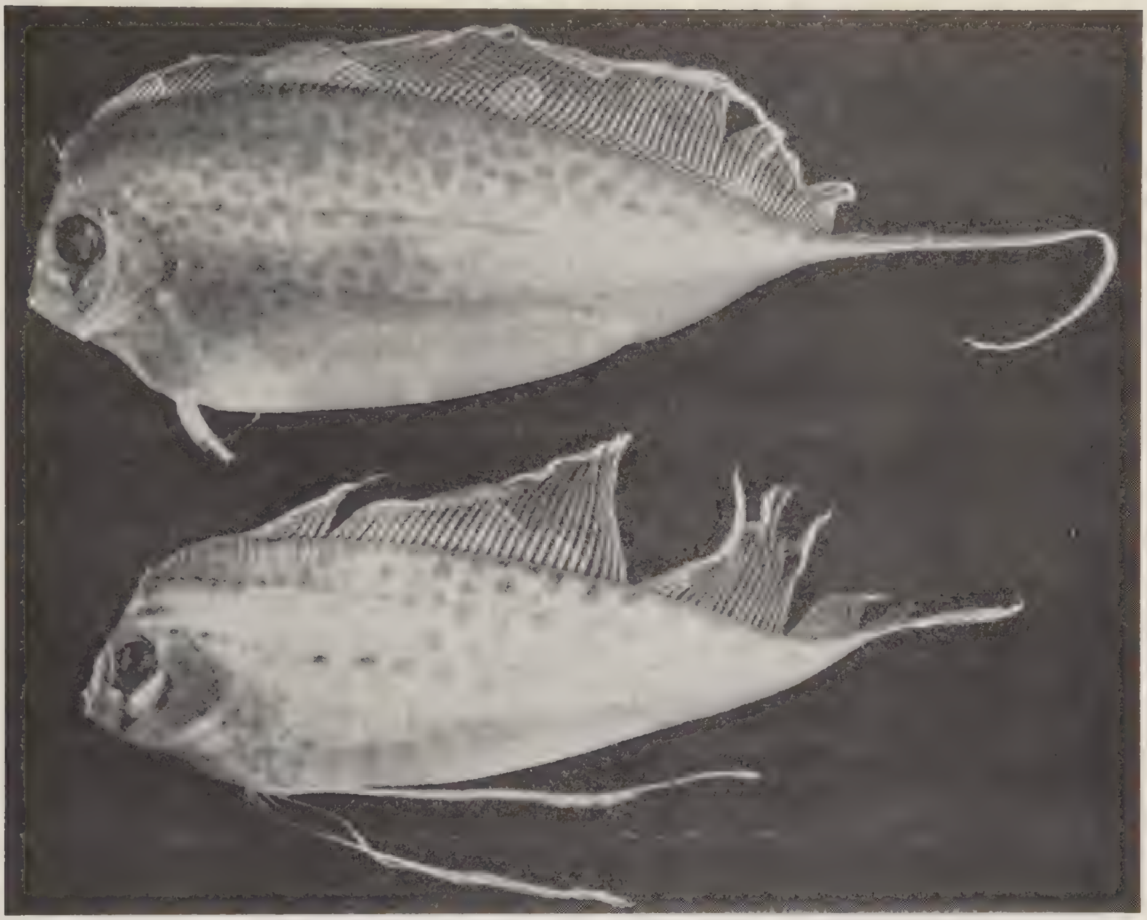

FIGURE 4.—Prejuveniles of *Desmodema*. Upper figure *D. lorum*, LACM 30597-1, 87 mm SV, 188 mm SL. Lower figure *D. polystictum*, SIO 75-55, 88 mm SV, 125 mm SL.

lorum. Fourmanoir 1969:36. Legand et al. 1972:383.

Trachipterus trachyurus, not of Poey. Leapley 1953:236; Fort Lauderdale, Fla.

Diagnosis.—A *Desmodema* with 71-74 total vertebrae (18-20 precaudal and 37-42 before the anus), 7-10 (usually 8) caudal rays, snout length less than eye diameter, attenuate tail in juveniles and adults (Figures 3, 7), and scales absent at all sizes.

Description of adult (see also Tables 1-3).—Ventral profile of body almost straight to anus, then tapering to elongate tail. Dorsal profile rising in a gentle curve to a point a little less than 1 head length behind head, then tapering rapidly to a point about 1½ head lengths behind anus, then tapering more gradually along elongate tail section. Tail long and straplike, postanal length almost two-thirds of standard length. Anus on ventral midline.

Head 2.2-2.5 in snout-vent length, and about 1.3 in greatest body depth. Eye large, diameter slightly greater than snout length. Ascending processes of premaxillae extending back to a point over posterior third of eye.

Dorsal origin over preopercle, preceded by a thickening representing pterygiophores of first six dorsal rays of juveniles. First fin rays short, succeeding rays becoming rapidly longer to about point of maximum body depth, height of fin then increasing more slowly, with longest rays slightly before anus. Behind level of anus fin rays become

TABLE 1.—Regression parameters for selected morphometric characters in *Desmodema*; p = *polystictum*, l = *lorum*.

Characters	Species	Intercept	Slope	Correlation coefficient	*N*
SV vs. SL[1]	p	40.7	0.30	0.97	11
	l	54.8	0.19	0.97	8
HL[2] vs. SV	p	−1.95	0.29	0.95	15
	l	−1.02	0.28	0.98	15
Depth at pelvics vs. SV	p	8.72	0.30	0.97	15
	l	14.57	0.28	0.96	15
Greatest depth vs. SV	p	6.93	0.35	0.97	15
	l	10.66	0.35	0.97	14
Depth at anus vs. SV	p	−0.39	0.20	0.92	15
	l	5.16	0.20	0.97	15
Depth at caudal base vs. HL	p	−0.13	0.02	0.95	11
	l	0.65	0.03	0.78	8
Orbit diameter vs. HL	p	0.05	0.40	0.97	14
	l	0.09	0.36	0.98	15
Eye length vs. HL	p	−0.52	0.38	0.96	14
	l	−0.46	0.33	0.99	14
Snout vs. HL	p	−1.19	0.38	0.99	15
	l	−1.50	0.42	0.93	15
Maxillary length vs. HL	p	0.65	0.37	0.99	15
	l	0.44	0.38	0.99	15
Maxillary width vs. HL	p	−2.27	0.34	0.96	15
	l	−2.81	0.34	0.96	15
Interorbit vs. HL	p	0.31	0.23	0.96	13
	l	−0.56	0.26	0.71	15
Pectoral-pelvic origin vs. HL	p	4.10	0.25	0.97	15
	l	8.07	0.23	0.75	14
Pectoral length vs. HL	p	4.26	0.32	0.95	12
	l	6.69	0.21	0.97	8
Longest dorsal ray vs. HL	p	19.66	0.31	0.81	11
	l	2.90	0.88	0.94	12

[1] SV = Snout vent length, SL = Standard length.

[2] HL = Head length.

TABLE 2.—Caudal and pectoral rays in *Desmodema*.

	Caudal rays							
Species	4	5	6	7	8	9	10	$\bar{x}$
D. polystictum				5	8	1	1	7.9
D. lorum	1	1	9	1				5.8

	Total pectoral rays					
Species	23	24	25	26	27	$\bar{x}$
D. polystictum		5	3	6	2	25.3
D. lorum	2	7	2	3		24.4

rapidly shorter, then fin margin even to caudal base. Pelvics absent but with buried bases still evident. Pectorals low, their bases almost horizontal, outline pointed, tip probably extending almost to lateral line when fin is intact.

Color in alcohol dark brown. Dorsal fin clear, becoming dusky, then black along tail. Caudal black. Pectoral clear. Iris dark, with a golden ring around pupil. In life the fish is silvery with dark red tones dorsally and on the head, and the fins red, except that the dorsal rays along the tail extension are black.

Description of prejuvenile.—Ventral profile of body sloping gradually down from tip of lower jaw to pelvic, then tapering in a gentle curve back to beginning of narrow tail section. Vent asymmetrical, opening on left side. Dorsal profile of head steep, but less so than in *D. lorum* of the same size. In the 44-mm SV individual, the profile is almost vertical to the dorsal origin, but in larger juveniles the slope is gentler, and slightly rounded above the eyes.

Dorsal profile of body curved from dorsal origin to over opercle then tapering back to tail. Point of maximum body depth just behind pelvic bases. Tail extension thin, but relatively short; postanal length about one-quarter of standard length. The narrow part of the tail is characteristically curved upward, so that caudal fin points up and forward.

Head length about 4 in snout-vent length, about 1.6 in greatest body depth. Eye diameter slightly greater than snout length. Ascending processes of premaxillae end over anterior third of eye. Dorsal origin over middle of eye, first five or six dorsal rays elongate, remainder of fin much as in adults.

Pelvic fins present, close together, origin level

TABLE 3.—Vertebral counts in *Desmodema*.

	Precaudal								
Species	18	19	20	21	22	23	24	25	$\bar{x}$
D. polystictum	1	3	3						19.3
D. lorum				2	6	9	2	2	22.8

	Preanal												
Species	37	38	39	40	41	42 . . .	46	47	48	49	50	51	$\bar{x}$
D. polystictum	1	3	1	1	—	1							38.5
D. lorum							3	5	—	5	3	1	48.2

	Total									
Species	71	72	73	74 . . .	106	107	108	109	110	$\bar{x}$
D. polystictum	4	2	—	1						71.7
D. lorum					2	—	2	2	2	108.5

with rear end of pectoral base. Orientation of fin bases and shape of rays as described for *D. lorum*. Pelvics frayed in all specimens, but reaching beyond end of caudal in one and to caudal base in another.

Color in alcohol pale, with a dusky area above and behind head, extending over forehead and anterior to snout tip. Ventral parts of head dusky, a dark streak below eye, running down behind maxilla, a dusky streak along throat to pelvic base. Body with conspicuous black spots which are somewhat larger and more widely spaced posteriorly and above midline. No spots conspicuously larger than others. A narrow dark streak on back along dorsal base, running out to caudal base. Probable life colors, based on two frozen specimens, silver with black spots; iris silver and the dorsal and caudal red; pectorals with pink tinge. This coloration corresponds well with that of the figure given by Tanaka (1908) except that the iris is shown by him as green. Smaller individuals differ (our smallest 32 mm SV) mainly in that the body is less deep and the ventral profile nearly straight, and there are no polka dots. The 37.5-mm SV holotype of *T. deltoideus* was described as "uniform bright silvery." A 55-mm SL individual in poor condition has traces of spots.

Remarks.—Leapley (1953) figured and described a Florida specimen of *D. polystictum* under the name *Trachipterus trachyurus* Poey 1861. The identification was based on the presence of 76 dorsal rays in Leapley's specimen, Poey's specimen having been reported to have 82 dorsal rays.

Leapley's photograph is of a *Desmodema* with a large eye and a relatively deep tail, in agreement with *D. polystictum*. No vertebral counts were given, but Frank Schwartz (pers. commun.) has supplied vertebral counts for Leapley's specimens, as well as an additional individual from the western North Atlantic. Both have 18 precaudal vertebrae, also in agreement with *D. polystictum*.

If Leapley's identification were correct, Poey's name would be a senior synonym of *Desmodema polystictum* (Ogilby 1897). However, three characters indicate that *D. polystictum* cannot be identified with *T. trachyurus*. These are number of ventral rays (6 in *trachyurus*, 8 or 9 in *polystictum*), pectoral rays (15, vs. 12-14), and coloration (silvery with a midlateral yellow band vs. polka-dotted). In addition, *T. trachyurus* was described as having vertebral processes piercing the skin (probably an artifact caused by postmortem drying) and lacking elongated anterior dorsal rays (present in all juvenile trachipterids).

The supposed agreement in low number of dorsal rays is invalid, since Leapley's specimen was broken far in advance of the caudal. Using his value for body depth of his specimen (141 mm) we estimate the actual length to have been between 1,400 and 1,500 mm. Poey's description does not allow the identification of *T. trachyurus* with any known trachipterid. *Zu cristatus* is excluded because juveniles of that form are strongly barred and have peculiar fleshy abdominal lobes that are unlikely to go unmentioned in a description.

The species of *Trachipterus* are not completely understood, but juveniles of that genus have dark markings, a dorsal pennant, and tubercles along the venter.

Material examined.—Western and Central Pacific: CAS SU 23783, Sagami Bay 1(72.8, 102.5); CAS 5532, Rurutu, Tubuai Islands 1(37.5, 49.9), holotype of *Trachipterus deltiodeus*. Eastern Pacific: UCLA W58-103, 96 km southwest of Cabo San Lucas, Baja California, tuna purse seine, 2(66, 91 and 88, 125); SIO 70-142, 19°50′N, 106°15′W, tuna purse seine, 1(260); SIO 68-33, 19°53′N, 110°46′W, "5 × 5" nekton net towed at 5 knots, 800 m wire out, 1(333, 1,040); SIO 63-915, 16°01.5′N, 100°54′W, "5 × 5" nekton net, 0-200 m, 1(277, 785); SIO 76-167, 12°55′N, 90°54′W, tuna purse seine, 1(111.5); SIO 76-294, 12°35′N, 92°15′W, tuna purse seine, 1(84.9, 126.5); SIO 76-67, 12°15′N, 92°25′W, tuna purse seine, 1(42); UCLA W67-135, 11°48′N, 88°25′W, 1(60 SL); SIO 73-392, 11°18′N, 91°31′W, tuna purse seine, 1(91.5); SIO 75-139, 10°00′N, 119°00′W, midwater trawl, 0-50 m, 2(74.3, 100.5 and 90 SL); SIO 76-325, 10°24′N, 107°46′W, midwater trawl, 225 m wire out, 1(25.5); SIO 73-400, 08°41′N, 85°03′W, dipnetted at surface, 1(82); SIO 64-397, 03°18.4′N, 101°54.3′W, stomach of *Alepisaurus ferox* 1(55.5); SIO 63-299, 04°03′N, 80°46′W, meter net, 400 m wire out, 1(23); SIO 75-590, 00°00.2′S, 119°17.0′W, meter net, 0-200 m, 1(28.0, 36.0); SIO 52-334, 02°47′S, 112°13′W, meter net, 0-250 m, 1(29, 40.5); SIO 73-340 "Eastern N. Pacific," tuna purse seine, 1(296, 835).

Desmodema lorum n.sp.

Figures 3, 4, 5, 6

Desmodema polysticta, not of Ogilby. Fitch

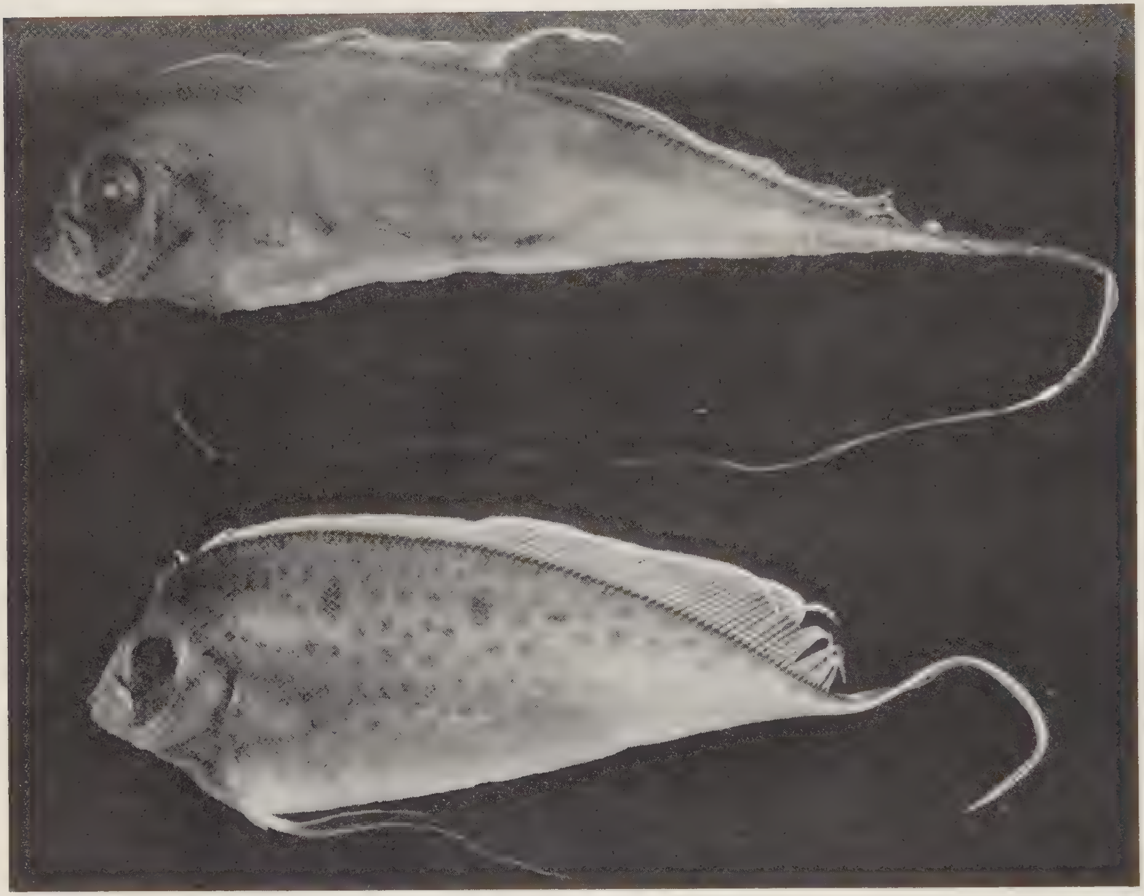

FIGURE 5.—Juvenile and prejuvenile of *Desmodema lorum*. Upper figure juvenile, LACM 35237-1, 103.7 SV, 412 mm SL. Lower figure prejuvenile, LACM 30230-1, 95 mm SV, 198 mm SL.

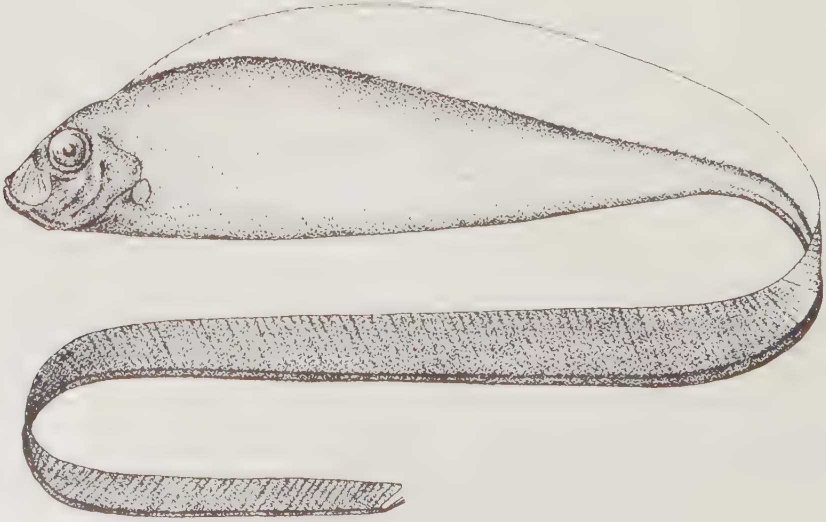

FIGURE 6.—Holotype of *Desmodema lorum*, USNM 216726. Fins reconstructed.

1964:321; in part, all but 10th, 12th, 13th of listed specimens (fig. 2 is *D. lorum*, fig. 3 is *D. polystictum*).

Desmodema polystictum, not of Ogilby. Berry and Perkins 1966:668. Fitch and Lavenberg 1968:88. Miller and Lea 1972:87.

Desmodema polystictus, not of Ogilby. Radovich 1961:18.

Diagnosis.—A *Desmodema* with 106-111 total vertebrae (21-25 precaudal and 46-50 before the anus), 4-7 (usually 6) caudal rays, snout length greater than eye diameter, an exceedingly long attenuate tail in juveniles and adults (Figures 3, 7) and scales present in prejuveniles and small juveniles.

Description of adult (see also Tables 1-3).—Ventral profile of body almost straight, but with a slight convexity back to anus, then tapering back to elongate tail section. Dorsal profile rising rapidly from snout tip to dorsal origin, then ascending more gently to maximum depth of body about one-half to three-quarters of head length behind head, then tapering back to tail. Tail exceedingly long and narrow, postanal length three-quarters of standard length. Anus on ventral midline.

Head length 3.2-3.8 in snout-vent length, 1.2-1.3 in greatest body depth. Eye moderate, equal to or (usually) shorter than snout. Ascending processes of premaxillae ending over or behind rear margin of eye. Dorsal origin just behind preopercle to over middle of opercle, preceded by a horny process representing pterygiophores of first six dorsal rays. First few dorsal rays short, succeeding rays becoming longer, with maximum height of fin over and posterior to anus. Fin height decreases gradually along tail, probably as reconstructed in Figure 6. Pelvics absent, but with buried bases still evident. Pectorals low, their bases horizontal. Pectoral pointed, but tip frayed and broken in all specimens.

Color in alcohol tan. Dorsal fin clear, becoming dusky, then black along tail. Caudal black. Pectorals clear. Iris dark with a golden ring around pupil. In life, probably silvery with red tones dorsally and on the head, and with the fins red.

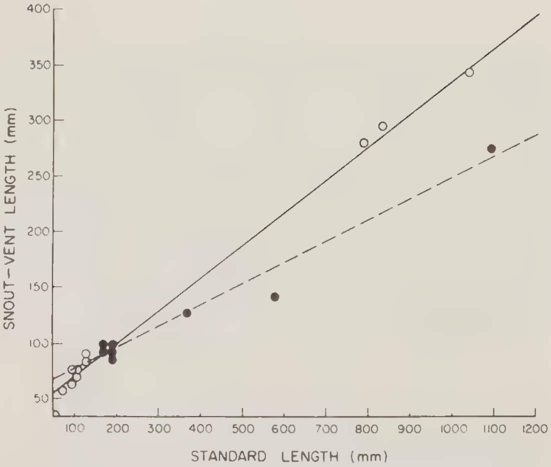

FIGURE 7.—The regression of snout-vent length on standard length in *Desmodema*. Open circles *D. polystictum*, closed circles *D. lorum*.

Description of prejuvenile.—Ventral profile sloping down from tip of lower jaw to pelvics, then tapering convexly back to vent, then tapering more sharply to beginning of tail, then straight. Usually a notch in outline at position of vent, which is asymmetrical, opening on the left side. Dorsal profile of head steep, almost vertical in smaller specimens. Back curved, point of maximum body depth just behind pelvic base. Dorsal profile becomes straight along tail elongation. Tail long and thin, postanal length about one-half of standard length.

Head length 3.8-4.2 in snout-vent length, 1.8-2.2 in greatest body depth. Eye about equal to snout length. Because of the steepness of the forehead, the ascending processes of the premaxillae end over the anterior third of the eye.

Dorsal origin over middle to posterior third of eye. First five or six dorsal rays elongate, remainder of fin shaped much as in adult except that the rays along the elongate tail are not as long. Pelvic fins present, close together, origin under pectoral base. Anteroposterior axes of pelvics parallel with sides. Pelvics broken in all our material, but reaching beyond anus in one specimen. Pelvic rays flattened and bladelike basally, the first the broadest, becoming filamentous distally. Minute prickles along rays. Pectorals as in adults.

Color in alcohol tan, a darker area on back over and behind head, extending down over forehead onto snout. A variably developed dusky streak from lower margin of orbit down behind maxilla. A dusky streak along throat to pelvic bases. Spotting somewhat variable but spots becoming larger and more widely spaced posteriorly and above midline. Three of five specimens with two noticeably larger spots on upper back on middle-third of body (see Figure 4). A narrow dark streak on back at base of dorsal, broadening on narrow part of tail. Individuals of about 35 mm SV differ in that the body is not so deep, and there is little or no pigment. Also the dorsal is relatively higher. Our smallest specimen, 18.5 mm SV, has the back with a straight taper behind the head, the ventral profile more evenly tapering, and has scattered melanophores on the head and over the viscera. These probably represent the larval pigmentation.

Identification and remarks.—The characters given in the generic and specific diagnoses serve to distinguish *D. lorum* adequately from all known trachipterids. In addition to the characters given in the diagnoses, the two species of *Desmodema* differ in number of dorsal rays. The single *D. lorum* counted had 197 dorsal rays and three *D. polystictum* had 120, 124, and 121, respectively. Another feature is the height of the dorsal. Large *D. lorum* have proportionately longer dorsal rays than do *D. polystictum* of equivalent size (Figure 8, Table 1). Prejuveniles of *D. lorum* can most easily be distinguished from those of *D. polystictum* by their deeper body, and more rounded anteroventral contour (Figure 4).

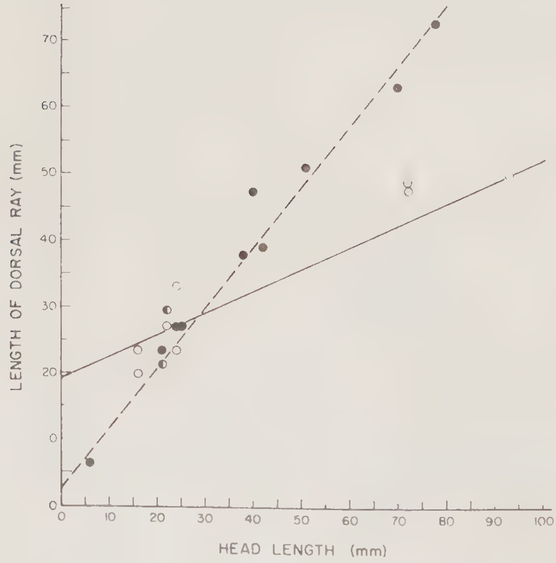

FIGURE 8.—The regression of length of longest dorsal ray on head length in *Desmodema*. Open circles *D. polystictum*, closed circles *D. lorum*.

Although Ogilby did not illustrate the holotype of *Trachypterus jacksoniensis polystictus*, his description is sufficiently detailed to allow identification with considerable certainty. The polkadotted coloration and lack of lower caudal lobe are diagnostic of *Desmodema*, and the dorsal ray count of 126 indicates that our material has been correctly assigned. The caudal count of seven or eight rays also accords with our concept of *D. polystictum*. Tanaka's (1908) excellent figure indicates that *Trachypterus misakiensis* has properly been synonymized with *D. polystictum*, and the presence of eight caudal rays in the small holotype of *Trachipterus deltoideus* dictates a similar placement.

Etymology.—From the Latin *lorum*, a whip, in reference to the elongate tail. Suggested common name, whiptail ribbonfish.

Material examined.—Holotype: USNM 216726, formerly SIO 62-434, a 1,098 mm SL (276 mm SV) male, taken between 29°05′N, 126°37′W and 29°03′N, 126°42′W by RV *John N. Cobb* with a Cobb Mk II trawl with 1,200 m wire out (estimated fishing depth 400 m) between 1930 and 2110 h on 25 August 1962. (Original station number 90.160, C6208, see Berry and Perkins 1966.) Paratypes: LACM 30217-1, 34°42′N, 121°20′W, spit up by *Thunnus alalunga*, 1(91.5, 167); LACM 9890-2, 34°25′N, 120°28′W, 15.2-m midwater trawl, 8 fm, 1(97, 173); LACM 9982, 33°00′N, 118°03′W, IKMT, 2,743 m wire out, 1(131); SIO 76-335, 13 km west of Oceanside, Calif., bait net, 1(95, 198); LACM 30597-1, 32°48′N, 118°16′W to 32°30′N, 118°30′W, IKMT, 1(87, 188); LACM 35237-1, 32°43′N, 118°57.5′W, 10-m midwater trawl, 1(103.7, 412); LACM 31678-1, San Clemente Island, Calif., off Pyramid Head, 1(83); LACM 30998-1, 31°45′N, 118°48′W to 31°44′N, 118°00′W, IKMT, 1,300 m, 1(93); SIO 63-375, 31°40.5′N, 122°03.5′W to 31°37.0′N, 122°04.3′W, Cobb Mk II trawl, 1,144 m wire out, 1(139.8, 580); SIO 63-429, 29°58.5′N, 120°07′W, IKMT, 4,500 m wire out, 1(173); LACM 9726-8, 29°29′N, 118°35′W, IKMT, 2,134 m wire out, 1(92.5, 189); SIO 74-47, 28°10.2′N, 160°00.9′E, IKMT, 0-1,000 m, 1(125, 364); UCLA W61-125, 64 km off Cabo Colnett, Baja California, 1(286), LACM 31800-2, 129 km south of Cabo San Lucas, Baja California, 1(283).

Additional material.—UCLA W55-320,

33°39′N, 135°00′W, 1; SIO 75-588, 29°17′N, 116°59′W, 1(55); UCLA A343, 28°N, 132°W, 1; UCLA W62-73, 32°10′N, 118°24′W, 1(53); SIO 75-589, 28°37.5′N, 118°18′W, 1(18.5); SIO 75-591, 33°34′N, 118°34′W, 1(89+ SL); LACM 31804, no data, 1(132); SIO 64-96, 31°39′N, 117°51′W, 1(289); SIO 72-16, 27°22′N, 155°23′W, 1(19.8, 26.4).

ACKNOWLEDGMENTS

We thank William Eschmeyer (CAS), Robert Lavenberg (LACM), and Boyd W. Walker (UCLA) for permission to examine specimens under their care. Gary L. Friedricksen turned three specimens over to us. John Fitch supplied collection data for certain specimens and read the manuscript. Robert Lavenberg and John Fitch supplied the original of the drawing of the holotype of *D. lorum*, first published in Fitch and Lavenberg 1968. Frank Schwartz, Institute of Marine Science, University of North Carolina, supplied vertebral counts of two Atlantic specimens of *D. polystictum*.

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MFR PAPER 1272

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A Review of the Yellowfin-Skipjack Tuna Fishery of the Atlantic Ocean and American Participation, 1956-75

GARY T. SAKAGAWA, ATILIO L. COAN, and TED C. MURPHY

INTRODUCTION

Over the past 2 decades the tropical tuna, or combined yellowfin tuna, *Thunnus albacares,* and skipjack tuna, *Katsuwonus pelamis,* fishery of the Atlantic Ocean has increased from a few hundred metric tons in 1956 to approximately 174,000 metric tons in 1975 (Fig. 1). It is currently the largest tuna fishery in the Atlantic Ocean and supports an international fleet of more than 800 vessels.

The vessels employed in the fishery are mainly longliners, baitboats, and purse seiners. They range in size from a few metric tons to 2,000 metric tons in carrying capacity. Longliners generally fish well offshore with longline gear (Shapiro, 1950) and catch deep-swimming tunas of frequently large size. Baitboats employ the pole-and-line with live-bait chum technique (Cleaver and Shimada, 1950), and purse seiners employ purse seine nets (McNeely, 1961). Both baitboats and purse seiners operate relatively close inshore and purse seiners also operate far offshore. They capture tunas, frequently of small size, that occur near the surface. Because of this difference in the type of tunas exploited by the different gears, the fishery is often divided for convenience into a longline fishery, consisting of longliners, and a surface fishery, consisting of baitboats and purse seiners.

The longline fishery extends throughout the tropical Atlantic, whereas the surface fishery is concentrated primarily off Africa (Fig. 2). Some areas in the western Atlantic, such as in the Caribbean Sea and off Venezuela, support a small surface fishery that is probably underdeveloped (Juhl, 1971; Ramos and Guerra, 1976; Wagner, 1974).

In this report we review the development of the tropical tuna fishery of the Atlantic from 1956 to 1975, and discuss the current condition of the stocks. Special attention is given to analysis of data from the American[1] tropical tuna fleet because this fleet is a relative newcomer to the fishery but ranks fourth in total production. Data sources for this study are: ICCAT (1976a) for data on catch and number of

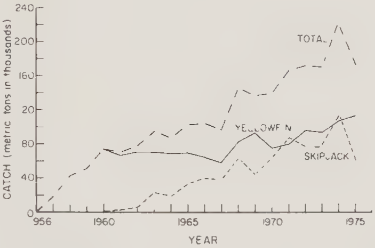
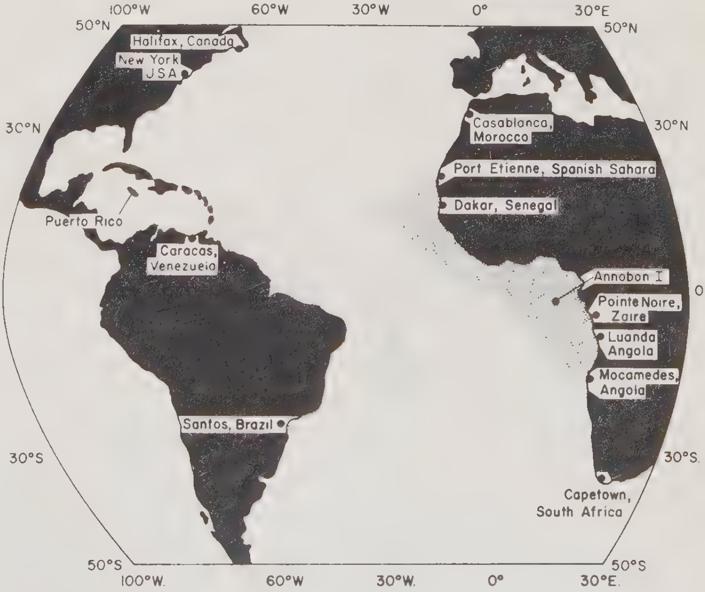


Figure 1.—Total Atlantic catches of yellowfin and skipjack tunas.

Figure 2.—Areas in the Atlantic Ocean where the longline fishery and surface fishery (speckled area in the eastern Atlantic) for tropical tunas are concentrated.



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[1] The combined tropical tuna fleets of Canada, Netherlands Antilles, Panama, and the United States are monitored as a unit. "American" in this report refers to this combined fleet, which during 1968-75 consisted of at least 83 percent U.S. vessels.

fishing vessels; Fishery Agency of Japan (1968-75) for data on longline catch and effort; and ICCAT (1973a, b, 1974a, b, 1975a, b) for data on sizes of fish caught and catch and effort of the surface fleets.

LONGLINE FISHERY

The longline gear is particularly effective in catching pelagic fishes that are widely dispersed in the open ocean. It is a multispecies gear but can be deployed to catch more of one species than another. In longline tuna fishing, albacore (*T. alalunga*), bigeye (*T. obesus*), bluefin (*T. thynnus* and *T. maccoyii*), and yellowfin tuna are primarily caught along with incidental catches of billfishes (Istiophoridae and Xiphiidae). Skipjack tuna is normally not caught on longline gear.

Longline fishing for tunas in the oceanic regions of the Atlantic Ocean was pioneered by the Japanese in 1956. In that year a few Japanese longliners conducted test fishing for tunas off the northeastern coast of South America (Shiohama et al., 1965). Fishing was excellent particularly for yellowfin tuna, and in the following year the fishery began in earnest with 26 Japanese longliners fishing throughout the tropical Atlantic. Additional Japanese vessels entered the fishery each year thereafter until the Japanese fleet peaked at about 210 vessels in 1965.

The catch rates for the Japanese fleet were initially high but quickly declined as the fleet rapidly increased in size. This caused some vessels to withdraw from the fishery and some to be sold to foreign interests, primarily to South Korean and Taiwanese fishermen. A few new, more efficient Japanese vessels entered the fishery as replacements while the former Japanese-owned vessels were placed into service by the new owners. The Koreans and Taiwanese found fishing in the Atlantic to be profitable and quickly acquired and deployed more vessels. Consequently, the international longline fleet grew rapidly in the late 1960's and early 1970's (Fig. 3). Currently, more than 500 longliners participate in the Atlantic tuna fishery with about 50 percent belonging to Korean and Taiwanese interests, about 40 percent to Japanese interests, and the remainder to Brazilian, Cuban, Panamanian, and Venezuelan interests.

Figure 3.—Number of vessels in the longline fishery of the Atlantic Ocean, 1956-73.

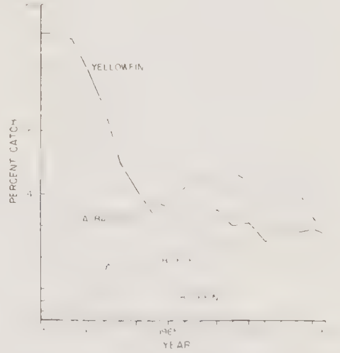

Figure 4.—Species mixture in the longline catch (tonnage) of the Atlantic Ocean, 1957-75.

Species Mixture

Before the mid-1960's, longlining in the Atlantic was primarily confined to tropical waters where the yellowfin tuna occur. Yellowfin tuna was the target species and contributed more than 30 percent of the total longline tuna catch (Fig. 4). The catch rate of yellowfin tuna, however, declined during this period and the fleet gradually shifted its operations to temperate regions in search of other species such as albacore and bigeye tuna (Shiohama et al., 1965). The species mixture of the catch, consequently, changed from primarily yellowfin tuna to primarily temperate tunas. Yellowfin tuna presently contributes less than 30 percent of the total longline tuna catch and albacore and bigeye tuna constitute more than 60 percent of the catch.

Yellowfin Tuna Catch and Catch Rates

Longliners were responsible for most of the catch of Atlantic yellowfin tuna before 1966 (Fig. 5); since then the surface fishery has produced most of the yellowfin tuna. The longline catch peaked at about 53,000 metric tons in 1960 and slowly declined to 21,000 metric tons in 1967. It then increased to about 30,000 metric tons in 1969 where it has remained.

More than 50 percent of the longline catch of yellowfin tuna was annually caught in the eastern Atlantic (east of long. 30°W) during 1957-64 (Fig. 6). About equal amounts were caught from the eastern and western Atlantic during 1965-69 and the bulk from the western Atlantic (west of long. 30°W) during 1970-75.

If there are two principal subpopulations (Honma and Hisada, 1971; Hayasi[2]), eastern and western subpopulations, of yellowfin tuna in the Atlantic Ocean, the longline catch rates suggest that the eastern subpopulation is more depressed than the western subpopulation (Fig. 7). The catch rate in the eastern Atlantic fell sharply from about 3.6 metric tons/1,000 hooks in 1958 to about 0.8 metric ton/1,000 hooks in 1962, and then gradually declined to less than 0.1 metric ton/1,000 hooks in 1975. In the western Atlantic it fell precipitously from about 3.3 metric tons/1,000 hooks in 1958 to about 0.7 metric ton/1,000 hooks in 1961 and then drifted lower to 0.4 metric ton/1,000 hooks in 1975.

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[2] Hayasi, S. 1973. A hypothesis on population structure of yellowfin tuna in the Atlantic Ocean, mainly based on longline data. ICCAT Collective Vol. Sci. Pap., 2 (SCRS-1973), p. 40-48.

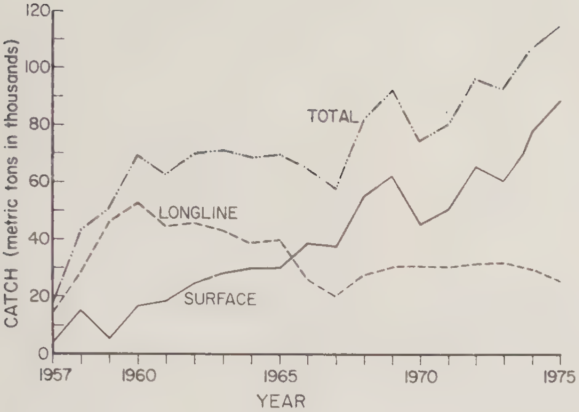


Figure 5.—Atlantic catches of yellowfin tuna for the longline and surface fisheries, 1957-75.

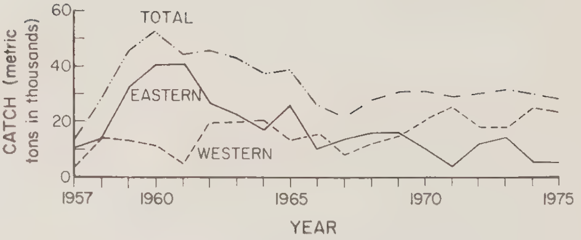


Figure 6.—Longline catches of yellowfin tuna from the eastern and western Atlantic, 1957-75.

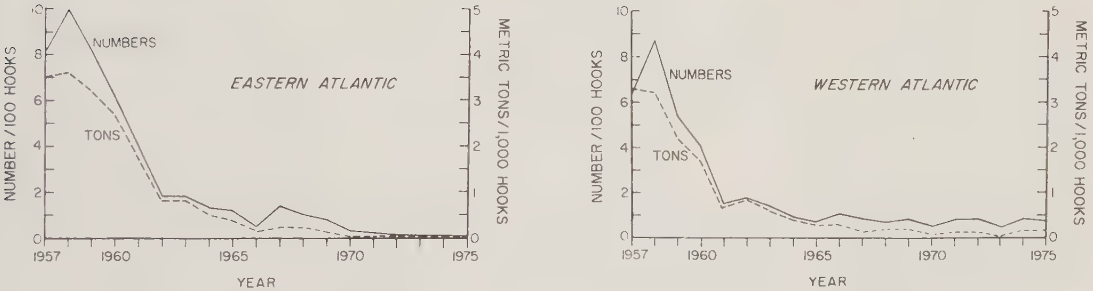
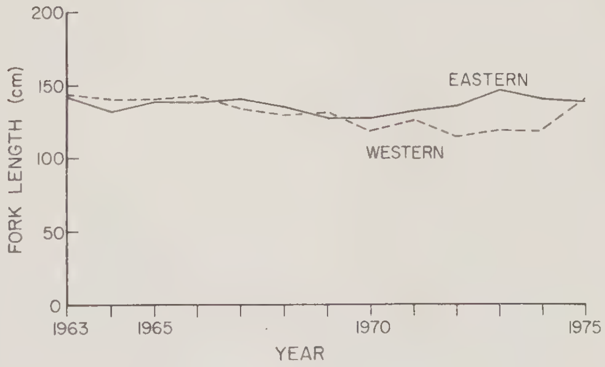


Figure 7.—Catch rates of yellowfin tuna for the Japanese longline fleet by eastern and western Atlantic.

Size Composition of Yellowfin Tuna

Before 1970, yellowfin tuna caught in the eastern and western Atlantic by the longline fishery were, on the average, about the same size (Fig. 8). Since the, the average size of fish caught in the western Atlantic has consistently been smaller. The average size of fish caught in the eastern Atlantic furthermore has remained quite constant despite the competition from the surface fishery that lands substantial numbers of large yellowfin tuna (>85 cm, Fig. 9). These data suggest the possibility that the longline and surface fisheries do not exploit the same stock (Lenarz and Zweifel, in press) and that in the western Atlantic the longline fishery is exploiting greater amounts of yellowfin tuna from the surface stock than the deep-water stock.

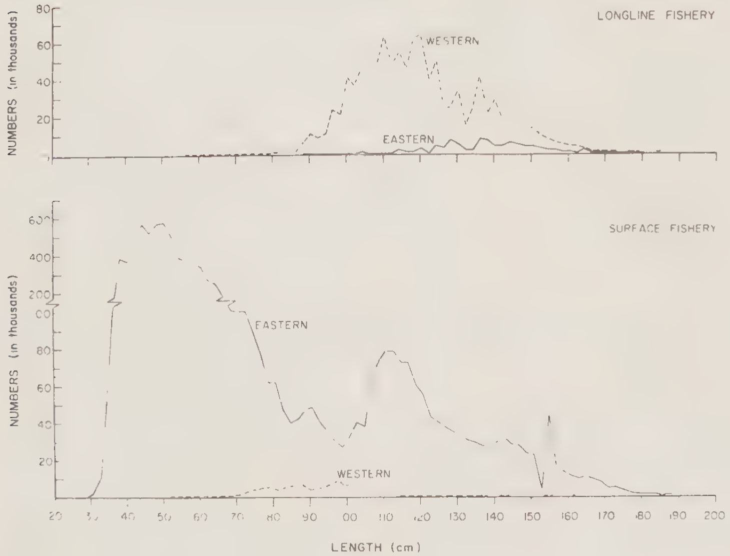
Figure 8.—Average fork length of yellowfin tuna caught in the longline fishery of the eastern and western Atlantic.



SURFACE FISHERY

Yellowfin and skipjack tunas are caught with surface gears in both the eastern and western Atlantic. The principal fishing areas are within 200 miles of the coast and currently most of the

Figure 9.—Estimated length composition of yellowfin tuna caught in the longline and surface fisheries of the Atlantic Ocean in 1974.



Atlantic catch is caught in the eastern Atlantic off Africa.

The eastern Atlantic surface fishery was an artisanal fishery up to about 1955. In that year, French baitboats from southern Europe moved into the Dakar, Senegal, region to fish for yellowfin tuna during November to May, when the boats were not employed in the albacore fishery off the Iberian peninsula (Champagnat, 1968). The boats were successful and baitboats of other countries soon entered the fishery. The fishery quickly expanded into southern waters and by 1960 the fleet was operating year-round from about Port Etienne, Spanish Sahara, to Pointe Noire, Zaire.

Purse seine fishing for tropical tunas, which was developed by U.S. Pacific coast tuna fishermen in 1956 (McNeely, 1961), was first tested in the Atlantic in the late 1950's. The technique was not seriously used in the Atlantic tropical tuna fishery, however, until 1961 by the French. Seiners of other countries soon thereafter entered the fishery. Currently more than 300 baitboats and purse seiners belonging to 12-15 countries participate annually in the eastern Atlantic fishery (ICCAT, 1976a). The largest fleet currently belongs to the combined French, Ivory Coast, and Senegal (FIS) countries.

Table 1.—Number of American tuna purse seiners[1] and their catches from the eastern tropical Atlantic, 1967-75.

		Catch (t)		Catch rate (t/day's fishing)	
Year	No. of vessels	Yellow-fin tuna	Skip-jack tuna	Yellow-fin tuna	Skip-jack tuna
1967	3	920	480	7.8	3.8
1968	8	5,830	3,180	23.3	12.0
1969	27	19,760	4,890	10.9	2.4
1970	25	9,810	11,790	4.0	5.1
1971	24	3,830	16,830	2.7	10.0
1972	36	12,100	12,250	3.3	3.7
1973	24	3,300	22,290	2.2	17.0
1974	26	5,620	19,970	2.8	8.7
1975	32	13,960	7,370	5.6	2.7

[1] The combined tropical tuna fleet of Canada, Netherlands Antilles, Panama, and the United States are monitored as a unit. "American" refers to this combined fleet which in 1968-75 consisted of at least 83 percent U.S. vessels.

Significant American participation in the Atlantic fishery began in 1967. In that year, three American tuna purse seiners fished off Africa and caught 1,450 metric tons of tuna in little over 2 months of fishing (Sakagawa and Lenarz, 1972). Their success attracted other American seiners into the fishery (Table 1). In 1975, 32 American tuna seiners participated in the eastern Atlantic fishery and their total catch was 13,960 metric tons of yellowfin tuna and 7,370 metric tons of skipjack tuna.

In the western Atlantic, the surface fishery for tropical tunas is small and not well developed. A few thousand metric tons are produced annually, principally by Cuban and Japanese baitboats, and French, Spanish, and American seiners. Cuban baitboats have fished primarily skipjack tuna in the Caribbean since 1932 (Suárez-Caabro and Duarte-Bello, 1961), whereas the other fleets are more recent participants and only occasionally fished in the western Atlantic for tropical tunas. American seiners of the tropical tuna fleet normally fish in the western Atlantic only while crossing the region enroute to Puerto Rico (to unload their catch) or fishing grounds in the eastern Atlantic and eastern Pacific. These vessels, therefore, do not spend many days searching for tunas in the western Atlantic. Because the surface fishery of the western Atlantic is small, this report does not attempt to fully discuss this fishery.

Species Mixture

Yellowfin and skipjack tunas are target species for the surface fishery. Yellowfin tuna, however, have traditionally been preferred by tropical tuna fishermen because it commands a higher market price. In fact, until recently some fishermen, particularly French fishermen, avoided the capture of skipjack tuna and caught them only incidentally with yellowfin tuna.

During the 1960's, when the catch rates of yellowfin tuna were high, an average of 56 percent of the total yellowfin-skipjack tuna surface catch from the eastern Atlantic was yellowfin tuna. As more units of fishing effort were applied to the fishery, the catch rates plummeted and the fishermen began relying more on skipjack tuna to fill their boats. The average percentage of yellowfin tuna in the catch declined to 42 percent during 1970-74.

Similar events occurred in the American catch (Table 1). Yellowfin tuna dominated the catch during 1967-69 and skipjack tuna during 1970-74. In 1975, however, skipjack tuna were

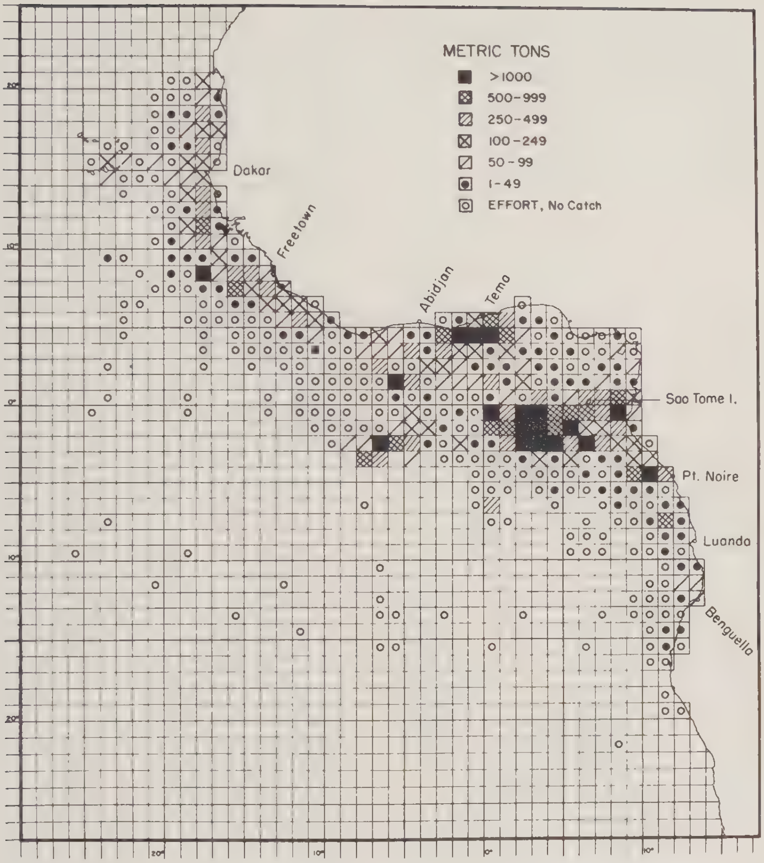


Figure 10.—Yellowfin tuna catch in 1° × 1° areas of the eastern tropical Atlantic. Logbook catches from the combined French, Ivory Coast, Senegalese, and American fleets for 1975 are shown.

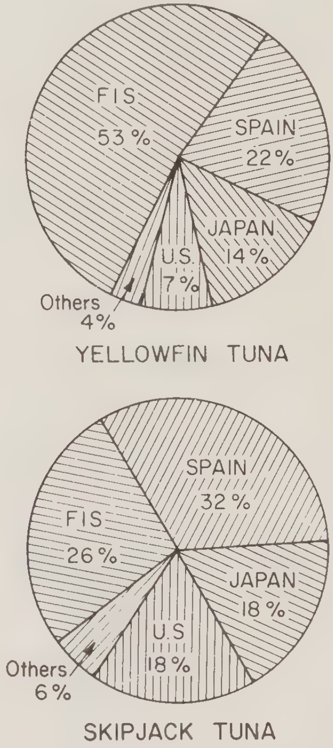


Figure 12.—Percentage of 1974 Atlantic catch of yellowfin tuna and skipjack tuna landed by major fleets. FIS fleet refers to French, Ivory Coast, and Senegalese boats.

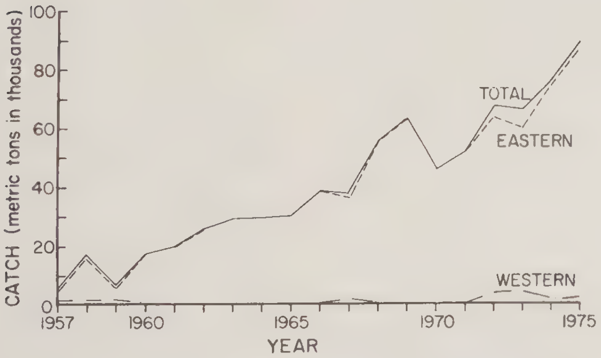


Figure 11.—Surface catches of yellowfin tuna from the eastern and western Atlantic, 1957-75.

scarce and American fishermen concentrated on catching yellowfin tuna. About 66 percent of that year's total catch was yellowfin tuna.

Yellowfin Tuna Catch and Catch Rates

The Atlantic surface catch of yellowfin tuna has fluctuated upwards at an average rate of 4,800 metric tons/year from 1957 to 1975 (Fig. 5). Since 1965 the catch has exceeded that of the longline fishery, and averaged 66 percent of the total Atlantic catch of yellowfin tuna.

Most of the Atlantic surface catch of yellowfin tuna is caught in the eastern Atlantic off Africa (Fig. 10). In 1975, about 99 percent of the catch was taken in the eastern Atlantic, primarily in the Gulf of Guinea (Fig. 11). About 96 percent of this catch was landed by the combined fleets of FIS, Spain, Japan, and the United States (Fig. 12).

Standardized catch rates for the eastern Atlantic fishery for yellowfin tuna were estimated by Coan and Fox[3]. Their estimates for the surface fishery are based on data from the FIS fleet and for the series of years 1964-75 (Fig. 13). The series of estimated catch per standard day at sea (SDA) show a peak of 4.7 metric tons/SDA in 1968, and a low of 2.1 metric tons/SDA in 1973 and 1975. Two periods, one of high and the other of low catch rates are also evidenced in the time series (Fig. 13). The period of high catch rates was during 1964-69 when the rates averaged 3.6 metric tons/SDA. Lower catch rates, averaging 2.3 metric tons/SDA, occurring during 1970-75.

Similar periods can be identified in the nominal catch rates of the American fleet (Fig. 13). Catch rates were well above 6.0 metric tons/day's fishing during 1967-69 and less than 6.0 metric tons/day's fishing during 1970-75. In both of these periods the American catch was made primarily in the third and fourth quarters of the year, and the highest yellowfin tuna catch rates were in the Gulf of Guinea (Figs. 14, 15).

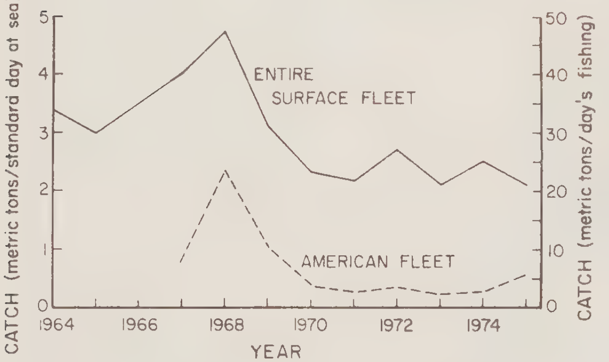


Figure 13.—Catch rates of yellowfin tuna caught in the surface fishery of the eastern Atlantic. Catch rates for the entire surface fleet (in metric tons/standard day at sea) and the American fleet (in metric tons/day's fishing) are shown.

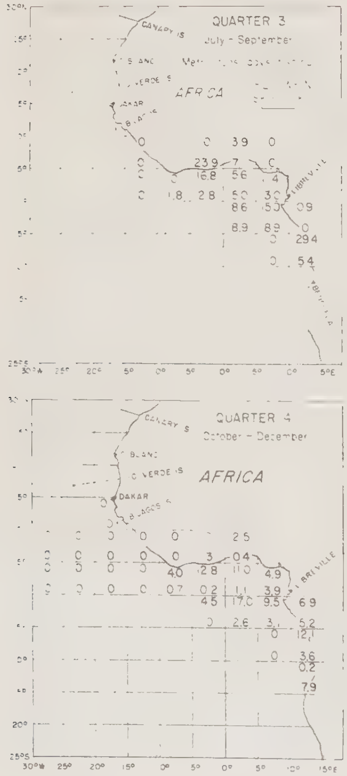

QUARTER 3
July - September
CANARY IS
AFRICA
QUARTER 4
October - December
C. BLANC
C. VERDE IS
AFRICA
DAKAR
BIJAGOS IS
LIBREVILLE

Figure 14.—Average catch rates of yellowfin and skipjack tunas in 5° × 5° areas by quarter caught by American seiners in 1967-69.

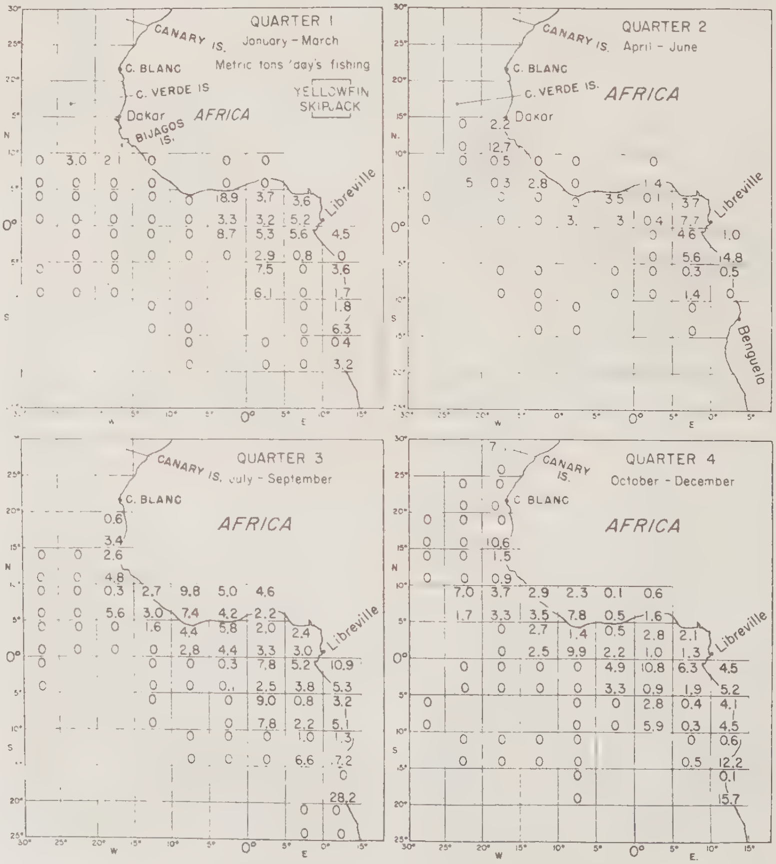

QUARTER 1
January - March
Metric tons/day's fishing
YELLOWFIN
SKIPJACK
CANARY IS.
C. BLANC
C. VERDE IS
Dakar
BIJAGOS IS.
AFRICA
Libreville
QUARTER 2
April - June
CANARY IS.
C. BLANC
C. VERDE IS.
Dakar
AFRICA
Libreville
Benguela
QUARTER 3
July - September
CANARY IS.
C. BLANC
AFRICA
Libreville
QUARTER 4
October - December
CANARY IS.
C. BLANC
AFRICA
Libreville
30°
25°
20°
15°
10°
5°
0°
N
S
W
E

Figure 15.—Average catch rates of yellowfin and skipjack tunas in 5° × 5° areas by quarter caught by American seiners in 1970-75.

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[3] Coan, A. L., and W. W. Fox. 1976. A production model analysis of the status of yellowfin tuna in the Atlantic Ocean, 1964-1975. NMFS, Southwest Fisheries Center, La Jolla, Calif., Admin. Rep. No. LJ-76-24, 16 p.

Yellowfin Tuna Size Composition

Size and age composition of yellowfin tuna in the surface catch of the eastern Atlantic was estimated by Coan[4]. His estimates show that fish between 31 and 125 cm long, or 1- and 2-year-olds made up the bulk of the catch in 1966-75. The dominant age group in most years was the 1-year-old (31 to 95 cm long—Fig. 9).

The average length of yellowfin tuna in the American catch ranged from 65 cm in 1971 to 111 cm in 1969 (Fig. 16). In all years except 1969, the dominant age group was the 1-year-old. In 1969 the dominant age group was the 2-year-old, probably resulting from the high percentage of catch from pure yellowfin tuna schools in that year (Sakagawa et al., 1976).

Skipjack Tuna Catch and Catch Rates

The catch of skipjack tuna from the Atlantic Ocean increased markedly between 1961 and 1975 (Fig. 17). The average rate of increase was about 10,000 metric tons/year with over 90 percent of the catch being taken in the eastern Atlantic. In 1975, the catch suddenly declined to approximately 59,500 metric tons from a peak in 1974 of about 114,700 metric tons. The cause of this sharp decline is believed to be due to poor availability, particularly off Angola in 1975.

Wide fluctuations in the catch have also been reported for other skipjack tuna fisheries, and they appear to be due to changes in availability and strength of year classes (Joseph and Calkins, 1969; Uchida, 1976). Oceanographic conditions are currently believed to be a major controlling mechanism for the fluctuations in availability of skipjack tuna (Williams, 1972).

Spanish, FIS, American, and Japanese tuna boats account for 94 percent of the total Atlantic catch of skipjack tuna (Fig. 12). Most of the catch is made in the Gulf of Guinea, off Senegal, and Angola (Fig. 18). In 1975, 70 percent of the total Atlantic catch of skipjack tuna was made in those areas.

Catch rates for skipjack tuna are

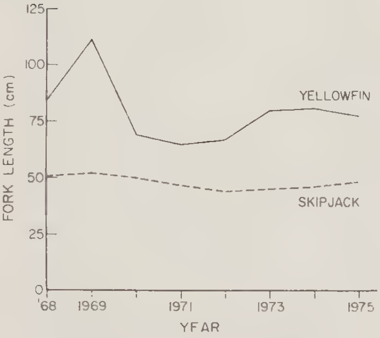


Figure 16.—Average fork length of yellowfin and skipjack tunas caught by American seiners in the eastern Atlantic.

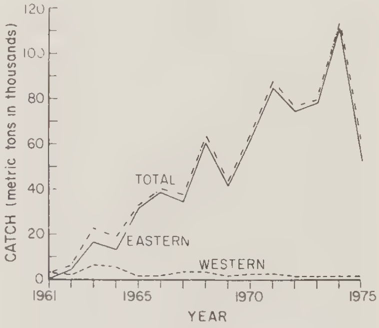
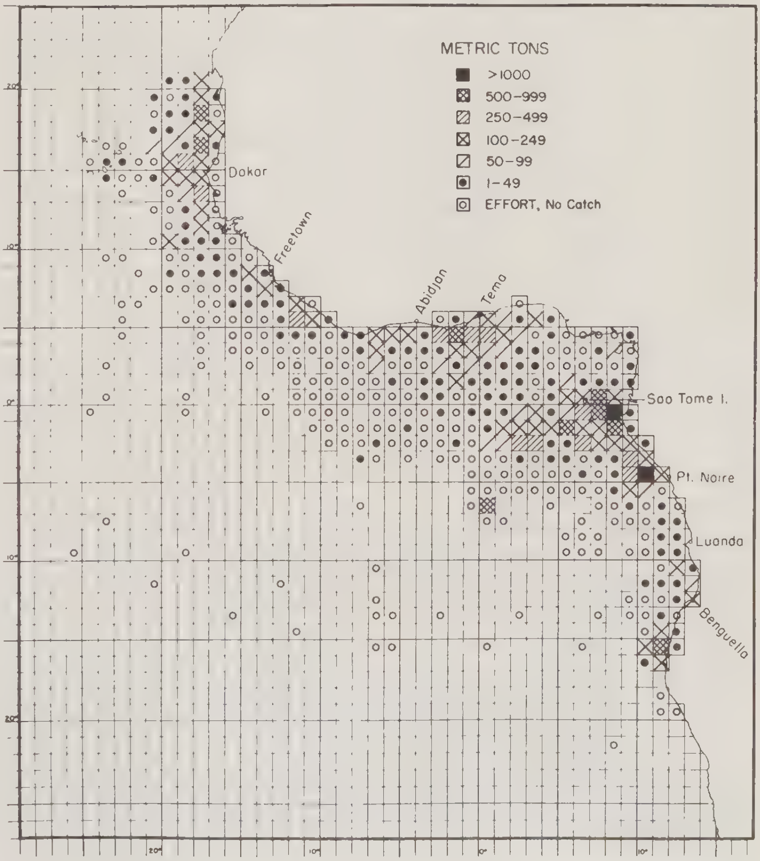


Figure 17.—Surface catches of skipjack tuna from the eastern and western Atlantic, 1961-75.

Figure 18.—Skipjack tuna catch in 1° × 1° areas of the eastern tropical Atlantic. Logbook catches from the combined French, Ivory Coast, Senegalese, and American fleets for 1975 are shown.



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[4] Coan, A. L. 1976. Length and age composition of yellowfin tuna from the Atlantic Ocean, 1966-1975. NMFS, Southwest Fisheries Center, La Jolla, Calif., Admin. Rep. No. LJ-76-22, 23 p.

quite variable. They are affected by the fishing gear, time and area fished, and whether skipjack tuna and not yellowfin tuna is the principal target species. A representative catch rate for the fishery is therefore difficult to estimate. Sakagawa and Coan[5] calculated standardized catch rates for the skipjack tuna fishery based on stratified nominal catch rates by vessel type and month, and by assuming that catch rates in the central part (Annobon) of the Gulf of Guinea (Fig. 2) were representative for the entire eastern Atlantic. Their estimates (Fig. 19) range from 1.2 metric tons/standard day's fishing in 1967 to 3.0 metric tons/standard day's fishing in 1971 and show peaks in 1971 and 1974. The 1975 estimate is 1.2 metric tons/standard day's fishing, or 43 percent below the estimate for 1974. This decline is less than the 52 percent decrease observed in the catch (Fig. 17), indicating that the stocks were not fished as hard as the decline in catch suggests.

Skipjack tuna catch rates for the American fleet are quite variable, but the trends are generally similar to those noted for the standardized catch rates of Sakagawa and Coan (Fig. 19). Most of the American catch of skipjack tuna since 1970, however, was made off Angola rather than in the Annobon region. The catch rates off Angola were exceptionally high in the third and fourth quarters of the year when most fishing by the American fleet took place (Fig. 15). High catch rates were also recorded in the first and second quarters in the Gulf of Guinea and off Senegal, but they occurred during the year when not much fishing by the American fleet took place. Consequently, they are not considered too reliable as indices of abundance.

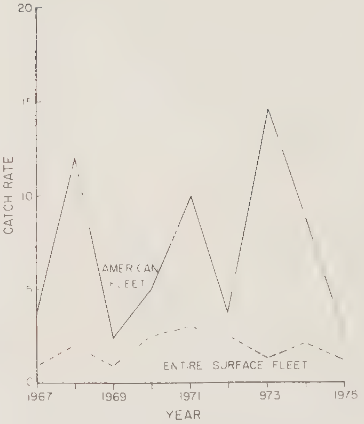

Figure 19.—Catch rate of skipjack tuna caught in the surface fishery of the eastern Atlantic. Catch rates for the entire surface fleet (in metric tons/standard day's fishing) and the American fleet (in metric tons/day's fishing) are shown.

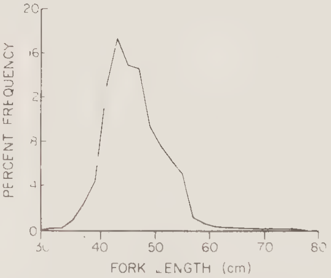

Figure 20.—Length frequency distribution of skipjack tuna caught in the eastern Atlantic in 1974.

Skipjack Tuna Size Composition

The Atlantic surface catch of skipjack tuna consists primarily of 30- to 60-cm long fish, or 1- and 2-year-olds (Fig. 20). For the past 5 years, 1-year-old fish (30 to 50 cm long) have dominated the catch, accounting for more than 50 percent of the numbers of skipjack tuna caught (Coan, 1976).

The American catch of skipjack tuna has likewise consisted of principally 1- and 2-year-old fish, with 1-year-olds dominating the catch (Sakagawa et al., 1976). The average length of fish in the American catch has fluctuated between a narrow range of 44-52 cm (Fig. 16).

STATE OF THE STOCKS

Production model analysis is commonly used in tuna stock assessments (e.g. Joseph, 1970; Skillman, 1975; ICCAT, 1976b). The analysis is usually based on catch-and-effort data from the fishery and relies on several assumptions, including: the model is applied to a closed, distinct, self-sustaining population; the concept of equilibrium conditions holds; and the age groups being fished remain constant. These assumptions rarely hold for tuna populations. Results from the analyses are consequently evaluated together with other information to determine the state of the stock.

Annual appraisals of the condition of Atlantic yellowfin and skipjack tuna stocks and fisheries are conducted by the Standing Committee on Research and Statistics of the International Commission for the Conservation of Atlantic Tunas (ICCAT). The appraisals have been based to a large extent on production model analysis.

Yellowfin Tuna

The most recent appraisal of the state of Atlantic yellowfin tuna stocks was made in 1976 (ICCAT[6]). The appraisal showed the stocks to be healthy and the catch increasing primarily because of offshore expansion of the surface fishery and strong recruitment of fish into the fishery. The maximum sustainable average yield (MSAY) was estimated to be 116,100 metric tons for the entire Atlantic fishery and 95,700 metric tons for the eastern Atlantic surface fishery only (Coan and Fox, footnote 3). These estimates were derived from a broad, flat-topped production model which indicate that only a negligible increase in equilibrium yield would result from further increases in fishing effort (Fig. 21). This conclusion has also been reached with yield per recruit models (Lenarz et al., 1974). The model also implies that at infinite fishing effort MSAY will be sustained from a reduced stock. This, of course, is impossible so conclusions drawn from extrapolation of the equilibrium yield curve too far to the right should be viewed with caution.

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[5] Sakagawa, G. T., and A. L. Coan. 1976. State of the skipjack tuna stocks of the Atlantic Ocean from production model analysis, 1969-1975. NMFS, Southwest Fisheries Center, La Jolla, Calif., Admin. Rep. No. LJ-76-25, 14 p.

[6] ICCAT. 1977. Proceedings of the fourth regular meeting of the council (Provisional), November 17-22, 1976. Int. Comm. Conserv. Atl. Tunas, Madrid, Spain, 121 p.

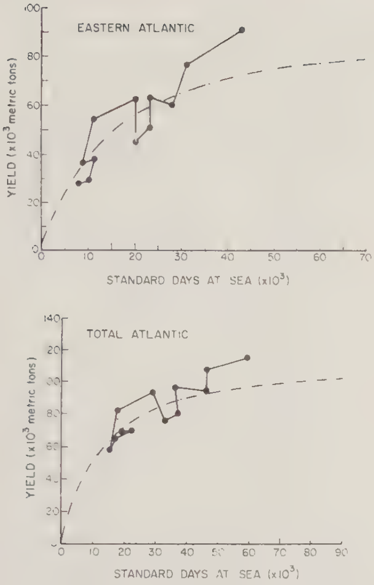

Figure 21.—Average yield curves and observed data, 1964-75, for the Atlantic fishery for yellowfin tuna.

A minimum size regulation is currently in effect for Atlantic yellowfin tuna that prohibits the taking of large numbers of fish less than 3.2 kg in size in excess of an incidental catch of 15 percent. The regulation was approved by ICCAT in 1972 to prevent reduction in the long-term yield through heavy exploitation of small fish. By 1974, most ICCAT countries had taken necessary legal action to implement the regulation. About 11,000 metric tons in 1974 and 4,000 metric tons in 1975 of undersized yellowfin tuna were caught by the eastern Atlantic surface fishery (ICCAT, footnote 6). The estimated losses to future yields from the removal of these undersized fish are approximately 10,000 and 4,000 metric tons. In other words, if the undersized fish were not caught in 1974 and 1975, they would have provided a total of 21,000 metric tons and 8,000 metric tons to the fishery in later years.

Skipjack Tuna

The catch of skipjack tuna from the Atlantic Ocean increased markedly during 1961-74, approaching crude estimates of potential skipjack tuna yields for the Atlantic (Sakagawa and Murphy, 1976). In 1975, however, fishermen experienced poor fishing for skipjack tuna and the catch reversed its upward trend, declining sharply by 47 percent. This was the largest decline recorded for the fishery and seemed to signal a decrease in stock abundance owing to fishing.

In 1976, ICCAT (footnote 6) reviewed the situation and concluded that the sharp decline in 1975 was due not to a decrease in stock abundance but to poor availability. It predicted that the catch would again be low in 1976 (about 40,000 to 50,000 metric tons) owing to fishing effort being diverted to catching yellowfin tuna.

Current estimates of MSAY for Atlantic skipjack tuna range from 89,300 to 118,400 metric tons for the eastern Atlantic surface fishery (Sakagawa and Coan, footnote 3). These estimates were derived from production models and are crude because satisfactory procedures to adjust the data to assumptions of the model have not yet been developed for Atlantic skipjack tuna. Nevertheless, the estimates indicate the general magnitude of the sustainable yield from the stock and that the yield can be quite variable because the fishery depends heavily on year classes that are available for only 1 or 2 years. Apparent natural mortality (biological and emigration), especially for fish older than 2 years, consequently, is high and there is no current need for instituting size or catch regulations for conservation purposes.

SUMMARY

The tropical tuna fishery is the largest tuna fishery in the Atlantic Ocean. In 1975, it produced approximately 174,000 metric tons of yellowfin and skipjack tunas.

The yellowfin tuna fishery is concentrated in the eastern tropical Atlantic. Growth of the fishery has been principally in the surface fishery since 1969, when the longline catch stabilized at about 30,000 metric tons. The stocks currently appear to be in good condition and capable of yielding larger catches but probably at a reduced catch-per-unit of effort.

The skipjack tuna fishery is also concentrated in the eastern tropical Atlantic. The catch reached a record high of 114,700 metric tons in 1974 then suddenly decreased to 59,500 metric tons in 1975. This decline apparently was due more to reduction in availability rather than reduction in abundance. The stocks currently appear to be in good condition. However, future catches can be expected to vary markedly, simply because skipjack tuna characteristically fluctuate widely in availability; the fishery is largely dependent on one or two year classes, which causes instability in production; and the amount of fishing effort exerted on skipjack tuna is dependent on availability and abundance of the co-target species, yellowfin tuna.

ACKNOWLEDGMENTS

Our sincere thanks to William H. Lenarz and David Kramer of the Southwest Fisheries Center for reading the manuscript and offering constructive criticisms. The paper has benefited from their keen eye for details and extensive knowledge of tuna fisheries. Any errors or lack of clarity in the paper, however, are solely the responsibility of the authors.

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Marine Biology 40, 317-325 (1977)

MARINE BIOLOGY

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Transfer of the Chlorinated Hydrocarbon PCB in a Laboratory Marine Food Chain

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Abstract

The transfer of chlorinated hydrocarbons (CHC) in a laboratory simulation of a three trophic level marine food chain was studied. The food chain consisted of the algal flagellate *Dunaliella* sp., the rotifer *Brachionus plicatilis*, and the larva of the northern anchovy *Engraulis mordax*. CHC were introduced into the seawater at concentrations representative of near-shore conditions off southern California without the use of dispersing agents. Each trophic level appeared to be in a steady-state at the time of first sampling, 5 days after inoculation. Apparent partition coefficients were calculated for each trophic level. The CHC contamination in the diet of the rotifers and anchovy larvae was also calculated. Unfed anchovy larvae accumulated the same amount of CHC as fed larvae and the final concentration appeared to be dependent on the CHC concentration in the seawater. The data in this report suggest that CHC accumulation is not a food-chain phenomenon but rather the result of direct partitioning of the compounds between the seawater and the test organisms.

Introduction

The presence of chlorinated hydrocarbons (CHC) in the marine environment has become a point of concern in recent years. Polychlorinated biphenyls (PCB) and pesticide residues have been detected in seawater (Cox, 1971; Harvey *et al.*, 1973; Bidleman and Olney, 1974; Pavlou *et al.*, 1974; Scura and McClure, 1975), sediments (Hom *et al.*, 1974; MacGregor, 1976), plankton (Cox, 1970; Risebrough *et al.*, 1972), fish (Zitko, 1971; MacGregor, 1974; Sims *et al.*, 1975), fish-eating birds (Moore and Tatton, 1965; Risebrough *et al.*, 1967), and marine animals (Addison *et al.*, 1973; DeLong *et al.*, 1973). CHC are accumulated by marine organisms because of the lipophilic nature of these compounds and an examination of the data show that, in general, members of the higher trophic levels contain relatively greater amounts of CHC. These observations support the conclusion that CHC are concentrated up the food chain (Woodwell *et al.*, 1967). However, information is scare concerning the mechanism of CHC transfer in marine food webs, particularly at the lower trophic levels.

Most investigators agree that the two principal means by which aquatic organisms accumulate CHC are by eating contaminated food or by a partitioning of the compounds directly from the water into the lipid of the organism until an equilibrium is established. The relative importance of these two routes of CHC accumulation has been discussed in several papers (Grzenda *et al.*, 1970; Macek and Korn, 1970; Hamelink *et al.*, 1971; Wildish and Zitko, 1971; Reinert, 1972; Södergren, 1973).

If equilibrium partitioning is an important route of CHC accumulation, then it is important that any laboratory demonstration of the transfer of CHC in an aquatic food web should have the test compound present in the water in a physical state similar to natural conditions and at concentrations known to exist in the environment. Many of the previous experiments which have been designed to demonstrate the uptake of CHC by aquatic organisms were conducted at CHC concentrations greater than the solubility of these compounds in water, and this could affect the apparent partition coefficient between the organism and the water (Butler, 1970). Most studies also used surface-active solvents such as acetone or methanol to keep the CHC in solution. If the accumulation of CHC by aquatic organisms is dependent on a partitioning of these compounds between polar and nonpolar phases, we believed it would be inappropriate to introduce even trace amounts of organic solvents which could affect the partitioning of CHC between phases.

In the research reported here we have studied the transfer of CHC in a laboratory simulation of a three trophic level marine food chain consisting of the algal flagellate *Dunaliella* sp., the rotifer *Brachionus plicatilis,* and the larva of the northern anchovy *Engraulis mordax.*

Materials and Methods

Introduction of CHC into Seawater and Media

CHC were introduced into seawater and culture media according to the method of McClure *et al.* (in preparation). This method relies on the fact that the atmosphere at La Jolla, California, USA, contains an average of 2×10^{-12} g/l CHC (predominately Aroclor® 1254). By bubbling laboratory air through 20 l glass carboys containing membrane-filtered (pore size, 0.45 µm) seawater or culture media, we introduced CHC into our experimental systems at concentrations similar to those found in samples collected near-shore off southern California (2.3 to 14.0 g $\times 10^{-9}$/l Aroclor® 1254 parts per trillion, pptr; Scura and McClure, 1975; McClure *et al.*, in preparation).

The air was passed through a glass inlet tube (3 mm inner diameter) which extended through a cork-stopper seal to the bottom of the carboy where it was fitted with an airstone. Air was filtered through a membrane filter (pore size, 0.45 µm) before it was bubbled through the seawater at a rate of 500 to 1,000 ml/min. The air exited through a glass tube (3 mm inner diamter) which passed through the cork stopper from above the water level.

The concentration of CHC in the air was monitored by passing a measured volume of air through a mineral oil air trap as described by McClure (1976). CHC were scavenged from the air by the mineral oil and subsequently eluted with *n*-hexane (all solvents were of nanograde quality and redistilled in glass). The CHC were separated from the mineral oil on a silica gel column and analyzed by gas liquid chromatography (McClure and LaGrange, 1976).

Analysis of Seawater for CHC

Seawater and media samples were analyzed for CHC according to the method of Scura and McClure (1975). One-liter samples were pumped through a copper column (100 mm x 5 mm inner diameter) containing an adsorbent which scavenged the CHC from the seawater. The adsorbent contained by weight 5% activated carbon powder, 10% MgO, and 85% refined diatomaceous earth. The CHC were eluted from the column with 10 ml of 30% benzene in acetone (v/v). The eluate was dried with Na_2SO_4 and interfering impurities were separated from the CHC on an alumina column (McClure, 1972). Pesticides were separated from PCB on silica-gel before analysis by gas liquid chromatography (GLC) (McClure, 1972).

CHC residues were analyzed on a Hewlett-Packard Model 5700 GLC with a ^{63}Ni electron capture detector. The glass column (2 mm inner diameter x 1.83 m) was packed with a commercially available solid phase (1.5% SP2250, 1.95% SP2401 on 100/120 Supelcon AW-DMCS). The oven temperature was set at 200°C, the injection port at 250°C, and the detector at 300°C. CHC were quantified by comparing retention time and peak area with known standards (McClure *et al.*, in preparation), and CHC identities were verified by comparing the R_f values from liquid-solid chromatography on silica-gel (McClure, 1972). Pesticide standards were provided by the Environmental Protection Agency, Perrine Primate Laboratory, Perrine, Florida, USA, and the PCB standards were supplied by the Monsanto Company, St. Louis, Missouri, USA. The chromatograms of our samples had a characteristic profile of peaks which was dominated by Aroclor® 1254. However, several other peaks were frequently present, including those corresponding to dieldrin, DDT and its metabolites and other unidentified compounds. Since the predominant CHC detected in our samples was Aroclor® 1254, we decided to follow the transfer of this compound in our experimental food chain. Unless otherwise indicated, the term PCB used in the text will refer to Aroclor® 1254.

Analysis of Tissue for CHC

Algal cells, rotifers, anchovy eggs and anchovy larvae were analyzed for CHC according to a modification of the method of Stanley and LeFavoure (1965). Five to 20 mg of dried tissue were digested in a 15 ml centrifuge tube for 2 h at 60°C in 8 drops of a mixture containing equal portions of glacial acetic acid and perchloric acid (60%). After the tissue was completely digested, 0.5 ml each of hexane, acetone and distilled water were added to the sample. The sample was thoroughly mixed and allowed to settle before the hexane-acetone fraction was removed. The tissue was extracted two more times with 0.5 ml of hexane; extracts were pooled and washed with 0.5 ml of distilled water. The solvent-CHC residue fraction was separated from the distilled water, evaporated just to dryness under vacuum at room temperature (ca. 20°C), cleaned on alumina, and the pesticides separated from PCB on silicagel before analysis by GLC (McClure, 1972). Recovery of standard Aroclor® 1254 using this procedure ranged from 92 to 98%.

Culture Methods

The green alga *Dunaliella* sp. was isolated from San Diego Bay (by A. Dodson); it was cultured in 20 l glass carboys in a medium described by Thomas (1964). The dinoflagellate *Gymnodinium splendens* was obtained from Dr. W.H. Thomas of the Scripps Institution of Oceanography; it was also grown in 20 l glass carboys in an enriched seawater medium containing soil extract (Lasker *et al.*, 1970), kept in constant light (500 to 700 ft-c) at 23° to 25°C, and continuously aerated. The rotifer *Brachionus plicatilis* was inoculated into the *Dunaliella* sp. cultures when the algal concentration reached 10^5 to 10^6 cells/ml. The combined cultures were maintained under the same conditions as the algae (Theilacker and McMaster, 1971).

Engraulis mordax eggs were collected from a spawning school maintained at the National Marine Fisheries Service, Southwest Fisheries Center (on occasion it was necessary to use hormones to induce spawning, according to the method of Leong, 1971). The larvae, reared in membrane-filtered seawater (pore size, 0.45 µm) in 10 l containers at 17°C (methods of Lasker *et al.*, 1970), started to feed on the third day after hatching; they were fed on the dinoflagellate *Gymnodinium splendens* for 2 days because their mouths were not yet large enough to feed on rotifers (Lasker *et al.*, 1970). The average concentration of PCB in the *G. splendens* was 0.6 ppm (dry weight). After the fifth day, and for the remainder of the experiment, the anchovy larvae were fed rotifers at a concentration of approximately 50/ml.

Sampling Procedures

Algal cells were collected in 1 l aliquots and counted with a Coulter Counter (Model B). The cells were separated from the medium in a KSB-R Servall Szent-Gyorgyi and Blum continuous-flow centrifuge in which all tubing and fittings containing plasticizers were replaced with PTFE Teflon parts. At 9,000 revs/min and a flow rate of 100 ml/min, all particles with a density greater than 1.1 and a diameter greater than 1.2 µm were removed from the seawater medium. The medium was analyzed for CHC as described earlier. The cell pellet was washed in 3% ammonium formate, pipetted into 15 ml centrifuge tubes and recentrifuged at 2700 revs/min in a Servall angle centrifuge. The supernatant fluid was carefully pipetted off; the cells were resuspended in approximately 1 ml of formate solution, pipetted onto a hexane-rinsed microscope slide and dried at 55°C to a constant weight. Losses of CHC using the above procedure ranged between 3 and 30% (recovery was determined by using ^{14}C-DDT as a tracer). No corrections were made in this report for losses.

The rotifers (99 to 281 µm long and 66 to 183 µm wide) were separated from the *Dunaliella* sp. (5 to 8 µm diameter) by slow sieving through a 35 µm Nitex® screen. *Gymnodinium splendens* (53 µm average diameter) was separated from its medium in the same manner through a 20 µm Nitex® screen. The rotifers and cells were washed on the screen with 3% ammonium formate, pipetted onto a hexane-rinsed microscope slide, and dried to a constant weight at 55°C. Dried tissue samples were scraped off the slide with a solvent-cleaned razor blade, weighed on a Cahn Electrobalance®, and transferred into 15 ml centrifuge tubes for CHC analysis.

Lipid Analysis

Percent lipid per unit dry weight was determined for rotifers and anchovy larvae. Dry tissue samples were ground in an agate mortar, placed in a 5 x 100 mm glass pipette with a glass-wool plug, and dried at 55°C to a constant weight. The samples were eluted with 10 ml of a chloroform-methanol solition (2:1 v/v). The samples were again dried to a constant weight at 55°C, and percent lipid was calculated.

Continuous Introduction of CHC into a Three-Step Food Chain

Areas of rapid phytoplankton growth in the ocean must also have some degree of mixing to replenish the nutrients utilized by the algae. This mixing will also replenish CHC as they are partitioned into the cells, resulting in a fairly constant concentration of CHC in the seawater. To duplicate these conditions in the laboratory, it is important to have a fairly constant input of CHC into the cultures.

We found that when *Dunaliella* sp. cultures were continually bubbled with air at a rate of about 500 ml/min, there was an increase in the total amount of PCB in the culture. The PCB levels in the algal cells remained relatively constant even during periods of rapid algal growth, and the amount of PCB taken up by the algae could always be accounted for by the amount of PCB lost from the medium and/or from the PCB entering the system from the bubbled air. In a typical 2-week experiment there were 3.6×10^{-9} g PCB in the air that was bubbled through a *Dunaliella* sp. culture each day (Fig. 1). The PCB concentration in the medium ranged between 2.3 and 3.1 pptr (g $\times$ 10^{-9}/l), and the algae contained from 0.17 to 0.23 ppm (parts per million). As the number of algal cells increased in the culture, PCB were partitioned onto the cells, resulting in an increase in the total amount of PCB in the culture.

Since algal cells were capable of taking up PCB in the manner described above, we used this technique to introduce CHC into a three-step food chain. *Dunaliella* sp. was cultured as described earlier while CHC were continuously introduced. Aliquots were removed every 5 days and the cells and medium were analyzed for CHC (Fig. 2). On Day 10, when the algal concentration had reached 10^5 to 10^6 cells/ml, rotifers were inoculated into the culture system. This two-step food chain (alga-rotifer) was sampled every 5 days; the rotifers were isolated from the algae and the medium. Each was analyzed for CHC. At every sampling, the volume (1 to 2 l), of the alga-rotifer culture removed was replaced with a dense suspension of *Dunaliella* sp. cells to maintain the initial algal concentration, thus insuring a healthy population of rotifers (Theilacker and McMaster, 1971). The concentration of PCB in the replacement algae was always within 0.15 ppm of the sampled algae. Starting on Day 25 of the experiment, rotifers were harvested every 1 to 5 days and fed to the anchovy larvae so that a concentration of approximately 50 rotifers/ml was maintained in the larval rearing containers. On Day 20 of the experiment, the anchovy eggs were sampled for CHC and they hatched later in the same day. The larvae were sampled again when they were 5 days old (Day 25 of the experiment) and every 5 days after that until the experiment was terminated on Day 45 when the larvae were 25 days old. Although we repeated this experiment three times, the results were not pooled because the CHC concentration in the cultures was dependent on the amount of CHC in the atmosphere which varied with time. In this report we present the results of our most complete test.

Results

The Accumulation of CHC in a Three-Step Marine Food Chain

The concentrations of CHC in the three trophic levels of our laboratory marine food chain are presented in Table 1. During the first 5 days, the number of *Dunaliella* sp. cells increased by 10-fold while the medium PCB concentration dropped from 13.1 to 2.6 pptr. Apparently, the amount of PCB introduced into the medium from the air at this time was not sufficient to keep up with the rapid uptake of PCB by the algae, so there was a decrease in the PCB concentration in the medium. However, the PCB concentration in the *Dunaliella* sp. cells remained fairly constant over the experimental period, ranging from 0.12 to 0.38 ppm (dry weight). *Brachionus plicatilis* averaged about twice as much PCB as the algae (0.29 to 0.54 ppm by dry weight). The PCB concentration in the *Engraulis mordax* larvae was also fairly constant (1.1 to 2.7 ppm by dry weight), and averaged about 5 times the level in the rotifers. DDT and DDE levels were barely detectable, but these results were included to demonstrate that other CHC were accumulated in a manner similar to PCB.

Apparently, PCB accumulation had reached a steady-state in each trophic level of this food chain by the time of first sampling on the fifth day after inoculation. If the source of PCB in the higher trophic levels was simply the result of a food-chain accumulation, the concentration of PCB in the animals should have increased with time. The fact that no such increase was observed suggests that the organisms depurated PCB directly into the water.

Dietary Sources of PCB Contamination

Information regarding the dietary sources of PCB contamination is important to an understanding of the processes involved in the transfer of PCB in a food chain. The amount of PCB in the diet of the rotifers was calculated according to the following argument. The work of Thei-

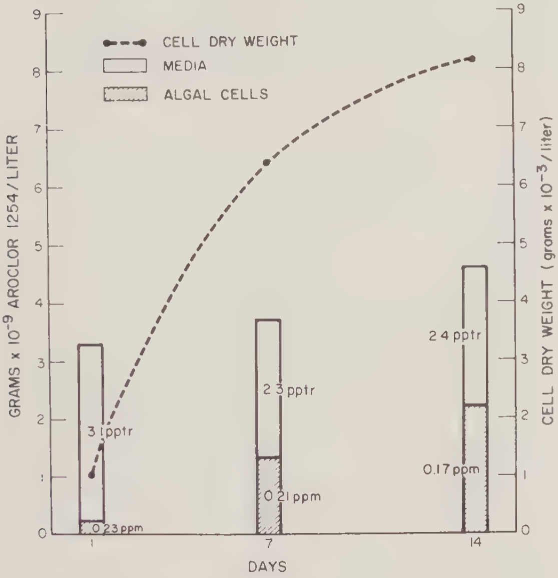

Fig. 1. Total amount of Aroclor® 1254 (PCB) in 1 l of *Dunaliella* sp. culture (includes amount in medium and cells, as indicated by height of bars) during exposure to bubbled air for 14 days. Open bars represent fraction of total PCB found in the medium; actual concentration of the medium is shown in parts per trillion (pptr). Portion of PCB associated with algal cells is depicted by cross-hatched bars and actual concentration is expressed in parts per million (ppm). Dry weight of algal cells in the culture is depicted on right ordinate

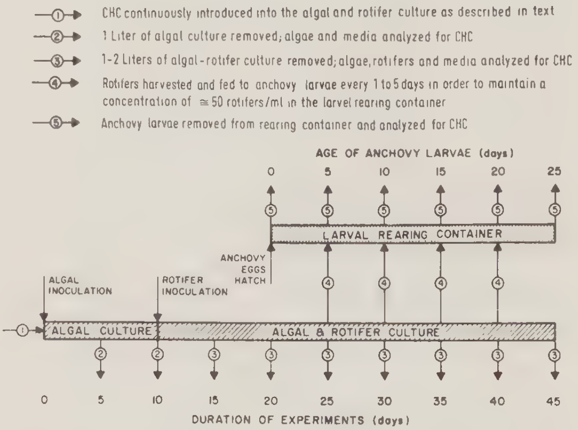
① CHC continuously introduced into the algal and rotifer culture as described in text
② 1 Liter of algal culture removed; algae and media analyzed for CHC
③ 1-2 Liters of algal-rotifer culture removed; algae, rotifers and media analyzed for CHC
④ Rotifers harvested and fed to anchovy larvae every 1 to 5 days in order to maintain a concentration of ≅ 50 rotifers/ml in the larval rearing container
⑤ Anchovy larvae removed from rearing container and analyzed for CHC
AGE OF ANCHOVY LARVAE (days)
0
5
10
15
20
25
LARVAL REARING CONTAINER
ANCHOVY EGGS HATCH
ALGAL INOCULATION
ROTIFER INOCULATION
ALGAL CULTURE
ALGAL & ROTIFER CULTURE
0
5
10
15
20
25
30
35
40
45
DURATION OF EXPERIMENTS (days)

Fig. 2. Flow-diagram of three trophic level food-chain experiment, depicting inputs into system and materials removed from system

Table 1. CHC concentration in three-step marine food chain

Medium (g x 10⁻⁹/l, pptr)				*Dunaliella* sp. (g x 10⁻⁶/g dry tissue, ppm)			*Brachionus plicatilis* (g x 10⁻⁶/g dry tissue, ppm)			Seawater in larval rearing container (g x 10⁻⁹/l, pptr)			*Engraulis mordax* larvae (g x 10⁻⁶/g dry tissue, ppm)		
Day	Aroclor® 1254	DDT	DDE	Aroclor® 1254	DDT	DDE	Aroclor® 1254	DDT	DDE	Aroclor® 1254	DDT	DDE	Aroclor® 1254	DDT	DDE
0	13.1	1.1	0.2	0.25[a]	0.02	ND									
5	2.6	0.6	ND	0.37	0.01	ND									
10	4.3	0.8	ND	0.25	ND	ND									
15	13.6	0.5	ND	Sample lost			0.54	0.02	ND						
20	6.6	1.0	0.3	0.28	0.01	ND	0.29	0.01	ND	2.0	ND	ND	0.35[b]		
25	8.0	0.3	ND	0.18	ND	ND	0.34	0.02	ND	*			1.93	0.18	0.29[c]
30	9.5	0.4	ND	0.12	ND	ND	0.49	0.02	ND	*			2.59	0.21	0.16
35	10.4	0.6	ND	0.16	ND	ND	0.51	ND	ND	*			1.11	Sample lost	
40	5.9	0.4	ND	0.38	ND	ND	0.42	0.02	ND	*			2.03	0.09	0.04
45							0.36	0.03	ND	*			2.67	0.09	0.01

[a] Inoculum.
[b] Anchovy eggs.
[c] 5-day old larvae were fed *Gymnadinium splendens* on Days 3 and 4.
*CHC determinations made on Day 20 only because of limited volume of seawater.
ND: Not detected.

lacker and McMaster (1971) indicates that the number of rotifers in a culture will double in 3 days at 24°C if the concentration of *Dunaliella* sp. remains at 10^5 cells/ml. The average weight of a single *Brachionus plicatilis* is 1.6×10^{-7} g (Theilacker and McMaster, 1971). Therefore, the average rotifer in a culture must assimilate at least 1.6×10^{-7} g from its food every 3 days in order to double in number. Obviously this is an overly simple explanation of events and the rotifers are not 100% efficient at converting *Dunaliella* sp. to rotifer tissue, but we have chosen this value because it results in the most conservative estimate of PCB uptake by the rotifers. In our experiments, the rotifers ate *Dunaliella* sp. which contained an average of 0.25 ppm PCB, and thereby ingested at least 1.33×10^{-14} g PCB/day. If the average rotifer assimilated all the PCB ingested it would accumulate a minimum of 0.08 ppm PCB each day or 0.42 ppm by Day 5. It seems possible, therefore, that the average rotifer could assimilate enough PCB from its diet to account for the levels detected in its tissue by the time of first sampling 5 days after inoculation. Since the level of PCB in the rotifers did not increase with time at this dietary level of PCB contamination, this indicates that a tendency toward equilibrium existed between the organism and the seawater and that PCB were also being excreted or partitioned out of the rotifer.

Similar calculations were made concerning the transfer of PCB from the rotifer to the anchovy larva. According to Hunter (1972), an *Engraulis mordax* larva between the age of 4 and 27 days makes an average of 1.28 strikes at rotifers per minute. The older the anchovy becomes, the more successful it becomes at capturing its prey. We used this information to calculate the number of rotifers eaten by an anchovy larva on Days 5, 10, 15, 20 and 25. Knowing the average concentration of PCB in the rotifers, the approximate amount of PCB eaten by a larva was determined (Table 2). To estimate the PCB accumulated at a particular age and dry weight, the amount of PCB eaten per day was ascertained by extrapolating between successive 5-day intervals and summing the daily PCB consumption.

According to these calculations, anchovy larvae could accumulate enough PCB from their diet by the age of 10 days to account for the levels detected in their tissue during the experiment, and these levels should have increased with time. However, no increase was observed; a steady-state seems to have been reached by the fifth day which was maintained throughout the remainder of the experiment.

Table 3 gives the average PCB concentration in the medium, algal cells, rotifers and anchovy larvae for the 45-day experiment. We have also calculated the amount of PCB in the lipid of these organisms, since virtually all the PCB in an organism are concentrated in the lipid. An apparent partition coefficient was calculated by dividing the PCB concentration in the lipid by the concentration in the seawater. When compared on a dry weight basis, there appears to be a biological magnification of PCB up the food chain, suggesting that higher members of the food chain accumulate PCB by eating members of lower trophic levels. This trend is not apparent when the PCB concentration is compared on a lipid basis. *Dunaliella* sp. lipid contained slightly more PCB than the rotifer lipid and, consequently, the partition coefficient between *Dunaliella* sp. lipid and seawater was greater than between rotifer lipid and seawater. What appeared to be bioamplification up the food chain when compared on a dry-weight basis was in reality only a reflection of the higher percentage of lipid in the rotifers.

However, the concentration of PCB in anchovy lipid was appreciably higher than in the lipid of the rotifers or the algae (Table 3). The partition coefficient between anchovy lipid and seawater was more than 20 times that of the algae or rotifers. Apparently, the percentage of lipid in an organism is not the only determinant of the amount of PCB accumulated by an organism. The chemical structure of the lipids of an organism might also affect partition coefficients. Grzenda *et al.* (1970) found that when goldfish (*Carassius auratus*) were exposed to 14C-DDT there was no correlation between the total lipid content of the various organ tissues and the residue concentrations. The authors interpreted this to mean that pesticides do not only accumulate in fat deposits. This finding could also be interpreted to mean that DDT has different solubilities in different types of lipids. Although it would be risky to conclude from our results that PCB are 20 times more soluble in anchovy lipid than they are in rotifer lipid, the following series of experiments do indicate that the higher concentration of PCB found in anchovy lipid was the result of equilibrium partitioning and not a food-chain phenomenon.

Table 2. *Engraulis mordax*. Calculated amount of Aroclor® 1254 (PCB) eaten by an anchovy larva

Age (days)	Average individual dry weight (g x 10^{-4})	Percent successful feeding strikes[a]	Feeding rate (organisms/min)[a]	No. of *Brachionus plicatilis* eaten per 14-h day	Dry weight of *Brachionus plicatilis* eaten per day (g x 10^{-5})	Aroclor® 1254 eaten/day (g x 10^{-11})	Aroclor® 1254 eaten/day (g x 10^{-11}; extrapolated)	Total Aroclor® 1254 eaten (g x 10^{-11})	Calculated concentration of Aroclor® 1254 in larvae (ppm)	Measured concentration of Aroclor® 1254 in larvae (ppm)
5	0.23	30	0.38	319	5.10	2.14	2.14 2.58 3.02 3.46 3.90	2.14 4.72 7.74 11.20 15.10	0.93	1.93
10	0.54	60	0.77	647	10.35	4.34	4.34 4.62 4.90 5.18 5.46	19.44 24.06 28.96 34.14 39.60	3.60	2.59
15	1.40	80	1.02	857	13.71	5.75	5.75 5.90 6.05 6.19 6.34	45.35 51.25 57.30 63.49 69.83	3.24	1.11
20	2.08	90	1.15	966	15.46	6.49	6.49 6.64 6.78 6.93 7.08	76.32 82.96 89.74 96.67 103.75	3.67	2.03
25	2.47	100	1.28	1075	17.20	7.22	7.22	110.97	4.49	2.67

[a] Data from Hunter (1972).

Table 3. Average concentration of Aroclor® 1254 (PCB) in dry tissue and lipid of algae, rotifers and anchovy larvae during 45-day food-chain experiment. Partition coefficients were calculated by dividing lipid concentration by medium concentration

Organism	Tissue concentration of Aroclor® 1254 (ppm)	Percent lipid	Lipid concentration of Aroclor® 1254 (ppm)	Medium concentration of Aroclor® 1254 (pptr)	Partition coefficient (x10^6)
Dunaliella sp.	0.25	6.4[a]	3.91	8.2	0.48
Brachionus plicatilis	0.42	15.0[b]	2.80	8.2	0.34
Engraulis mordax	2.06	7.5[b]	27.46	2.0	13.70

[a] Data from Parsons *et al.* (1961).

[b] Chloroform-methanol (2:1 v/v) extract.

Table 4. *Engraulis mordax*. Concentration of Aroclor® 1254 (PCB) in fed and unfed anchovy larvae. Partition coefficients were calculated by dividing lipid concentration by medium concentration

	Aroclor® 1254 by dry weight in eggs (ppm)	Aroclor® 1254 in seawater (pptr)	Aroclor® 1254 by dry weight in larvae (ppm)	Aroclor® 1254 in lipid of larvae (ppm)	Partition coefficient (x10^6)
Unfed 3-day old larvae	0.36	2.5	2.80	37.33	14.9
Unfed 2-day old larvae	0.33	4.5	4.70	62.67	13.9
Average of fed larvae over 25 days	0.35	2.0	2.06	27.46	13.7

Comparison of PCB Accumulation in Fed and Unfed Anchovy Larvae

In a final experiment, *Engraulis mordax* eggs of a known PCB concentration were hatched and the unfed larvae were analyzed for PCB content 2 to 3 days after hatching at the time when the yolk sac is absorbed and when they normally start feeding (Table 4). In one test, the eggs contained 0.36 ppm PCB (dry weight) and were hatched in seawater containing 2.5 pptr PCB. Three days after hatching, the unfed larvae contained 2.80 ppm PCB (dry weight). In another experiment, the initial concentration in the eggs was 0.33 ppm PCB (dry weight) and the seawater was 4.5 pptr. Two days after hatching the larvae contained 4.70 ppm (dry weight). In both tests, although the PCB concentration in the seawater and the larvae was different, the partition coefficient between the seawater and anchovy lipid was almost the same, which indicates that the PCB concentration in the larvae was dependent on the concentration in the seawater. Also, the partition coefficient of the unfed larvae was essentially the same as the partition coefficient calculated from the average PCB concentration in fed larvae from the three-step food-chain experiment. Again, this indicates that an equilibrium was established between the seawater and the larvae which was independent of the anchovy's position in the food chain.

Discussion and Conclusions

The concentration of PCB in each trophic level of a three-stop marine food chain (algae → rotifer → anchovy larvae) was monitored for 45 days. The dietary contamination to the higher trophic levels was calculated and it was determined that the PCB concentration in the food ingested was adequate to account for the residues found in the tissues of the organisms. When the PCB concentration was determined on a dry weight basis there appeared to be an amplification in a step-wise fashion up the food chain. However, when the PCB concentration was calculated on a lipid basis this trend was no longer apparent in the lower trophic levels. The algae and the rotifers contained essentially the same PCB concentration; what appeared to be a food-chain accumulation was really a reflection of the higher amount of lipid in the rotifers. This did not hold true for the higher trophic level; PCB residues in the lipid of the fish larvae were about 10 times higher than the invertebrates. Although this finding supports the theory of the bioamplification of pollutants up the food chain, we have contradictory evidence that suggests that anchovy larvae partition PCB directly from the seawater. We found that unfed anchovy larvae contained essentially the same amount of PCB as fed larvae and that the final concentration in the tissue was related to the amount of PCB in the water. Also, bioamplification suggests that the PCB concentration in an organism will increase with time if dietary inputs remain constant, but no such increase was observed in this study. Instead, all three steps of the food chain were in a steady-state by the time the first sample was taken.

The surface-area-to-volume ratio of first-feeding anchovy larvae is large enough to enable the fish to rely upon diffusion to take care of respiratory needs. Older fish maintain a large surface area of diffusive tissue in contact with the water by developing gills. Aquatic animals which rely upon diffusive interaction with the water for respiratory and metabolic needs will partition lipophilic compounds across these membranes and establish an equilibrium with the surrounding water which will depend on the concentration of the compound in the water and the solubility of the compound in the water and the lipid of the organism. It is our conclusion that this mechanism is the primary determinant of the CHC levels detected in exposed aquatic organisms.

Acknowledgements. We thank Drs. V.E. McClure and R. Lasker for many helpful discussions and Mr. G.W. Rommel for his assistance in all phases of this project. This work was supported by an NSF-IDOE grant No. GX-32977 to Dr. R. Lasker.

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Date of final manuscript acceptance: November 26, 1976. Communicated by J.S. Pearse, Santa Cruz

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VARIOUS SPECIES OF PHYTOPLANKTON AS FOOD FOR LARVAL NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, AND RELATIVE NUTRITIONAL VALUE OF THE DINOFLAGELLATES *GYMNODINIUM SPLENDENS* AND *GONYAULAX POLYEDRA*

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ABSTRACT

First feeding northern anchovy larvae were presented with a variety of phytoplankters common to coastal waters of southern California to determine which species are acceptable as food. Most of the larvae ate the four species of dinoflagellates tested in feeding experiments but did not feed on diatoms or small flagellates. Larval rearing experiments were conducted to compare the nutritional value of *Gymnodinium splendens* and *Gonyaulax polyedra*, two species of dinoflagellates readily eaten by anchovy larvae and known to predominate in the chlorphyll maximum layers off the southern California coast. *Gymnodinium splendens* was a nutritional food for the first 10 days of larval life, but *Gonyaulax polyedra* was judged to be inadequate. Supplementing the *G. polyedra* diet with microzooplankton increased larval survival comparable to survival on a microzooplankton diet alone. When the *Gymnodinium splendens* diet was supplemented with microzooplankton, the larvae grew faster but survival did not increase. Results are discussed in relation to studies on larval survival in the Southern California Bight during 1974 and 1975.

The strength of a year class of fish may depend on availability of food organisms during the early larval stages (May 1974). Consequently, there have been attempts to assess the abundance of planktonic organisms in larval feeding areas as a step towards predicting year class success (Shelbourne 1957; Bainbridge and Forsyth 1971; Lasker 1975, in press). For this approach to be successful, additional information is also necessary concerning: 1) selection of prey by the fish larvae, 2) concentration and size of food organisms necessary to initiate feeding by the fish larvae, 3) nutritional value of the food that the larvae select, and 4) temporal and spatial distribution of the food organisms in the feeding area.

The northern anchovy, *Engraulis mordax*, larva has been studied in the laboratory and many criteria for successful feeding have been determined (Lasker et al. 1970; O'Connell and Raymond 1970; Hunter 1972, 1976; Hunter and Thomas 1974). Results of these studies indicate that first feeding anchovy larvae require small particles (<100 μm in smallest dimension) at relatively high densities to initiate feeding and to insure moderate survival. O'Connell and Raymond (1970) found in laboratory experiments that anchovy larvae reared in seawater containing 1 copepod nauplius/ml or less experienced heavy mortalities during the sixth and seventh days after hatching. To date such a high concentration has not been found in the nearshore region of the California Current (Beers and Stewart 1967, 1969). However, the possibility does exist that anchovy larvae could survive on some of the larger phytoplankters during early stages of development (Hunter and Thomas 1974). Lasker et al. (1970) found that anchovy larvae would feed and grow to a length of 5 to 6 mm in the laboratory on a diet of the naked dinoflagellate, *Gymnodinium splendens*. With this in mind, Lasker (1975) used laboratory-spawned anchovy larvae to test for feeding activity in seawater pumped from the surface and chlorophyll maximum layer in the nearshore region of the Southern California Bight. Lasker found that during March and April 1974 there were sufficient numbers of *G. splendens* (>20 organisms/ml) in the chlorophyll maximum layer for initiation of feeding by anchovy larvae. During 1974 and 1975, Lasker (in press) monitored the plankton distribution off the southern California coast in an effort to establish a

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Manuscript accepted February 1977.

relationship between oceanographic conditions and larval anchovy food organisms. In 1975 he found that *G. splendens* was replaced as the dominant organism in the chlorophyll maximum layer by the armored dinoflagellate, *Gonyaulax polyedra,* and later by a variety of small diatoms. In an effort to assess effects that this succession might have on survival of anchovy larvae, we have conducted feeding experiments with some of the phytoplankters common in the Southern California Bight to determine which species are acceptable as food by anchovy larvae. In addition, we have examined the relative nutritional value of *Gymnodinium splendens* and *Gonyaulax polyedra.*

METHODS AND MATERIALS

Phytoplankton Cultures

The phytoplankters chosen for feeding experiments are common to southern California coastal waters, and most were major components of the chlorophyll maximum layers during 1974 and 1975 (Lasker in press). Also, they were of an appropriate size for ingestion by first feeding anchovy larvae (Table 1). Axenic cultures of the selected phytoplankters were supplied by James Jordan of the Food Chain Research Group at Scripps Institution of Oceanography. Culture techniques were described by Thomas et al. (1973).

TABLE 1.—Average dimensions of phytoplankters offered as food to first feeding anchovy larvae

BACILLARIOPHYCEAE	
Ditylum brightwellii (25 × 150μm, single cells)	
Chaetoceros affinis (4μm wide in chains to 200μm)	
Thalassiosira decipiens (8 × 10μm, single cells)	
Leptocylindrus danicus (5μm wide in chains to 75μm)	
DINOPHYCEAE:	CHLOROPHYCEAE
Gymnodinium splendens (51μm)	*Chlamydomonas* sp. (10μm)
Gonyaulax polyedra (40μm)	*Dunaliella* sp. (6μm)
Prorocentrum micans (27 × 38μm)	
Peridinium trochoideum (20μm)	

Feeding Experiments

To determine which phytoplankters are preyed upon by anchovy larvae, feeding experiments were conducted using methods similar to those of Lasker (1975). Cylindrical 8-liter battery jars, wrapped with dull black cardboard, were filled with approximately 5 liters of filtered seawater (filter pore size, 5 μm) and inoculated from a dense culture of the phytoplankton to be tested. The densities were determined by counting organisms in 1-ml alilquots in a Sedgwick–Rafter[3] counting chamber and/or with a Coulter Counter Model Ta, and the size was measured with an ocular micrometer. Experiments were conducted at temperatures ranging from 16.9° to 19.6°C, and the test jars were illuminated from above with a bank of four 40-W fluorescent lamps. Light intensity at the surface of the test jars was approximately 2,400 lx. Because anchovy larvae readily feed on *Gymnodinium splendens* (Lasker 1975), at least one container in each series of experiments contained only this food organism as a control to test the feeding ability of each batch of larvae.

Diatoms were maintained in suspemsion during the feeding trials by a gentle stream of bubbled air in each test jar. To evaluate the effect of such agitation on the ability of larvae to feed, experiments were conducted with and without bubbled air using *G. splendens* as food. Little effect on feeding ability could be detected (Table 2, Trial 1).

Anchovy eggs were obtained from adult anchovies maintained in spawning condition at the Southwest Fisheries Center Laboratory. Spawning techniques were described by Leong (1971). Anchovy eggs and larvae were allowed to develop in 1-liter jars (100 eggs/jar) containing filtered seawater (filter pore size, 5 μm). First feeding larvae (2.5 days after hatching at 17°C) were placed in the experimental containers with the test organism for approximately 8 h before being siphoned from the containers and quickly immobilized on a membrane filter (pore size, 8 μm) by vacuum filtration. This technique helped to prevent the larvae from defecating (Lasker 1975). The larvae remained somewhat transparent after air drying so that the presence of food in the gut could be determined by microscopic examination of the intact animal.

Larval Rearing Experiments

Anchovy larvae were reared for 10 days in 10-liter circular containers immersed in a temperature-controlled bath in an air-conditioned room (Lasker et al. 1970). The containers were filled with membrane filtered seawater (pore size, 0.45 μm), the salinity was 33.4‰, and the temperature was maintained at 16.0° ± 1.1°C. Lighting

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[3] Mention of trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Laboratory feeding experiments showing the percentage of anchovy larvae that fed on: 1) diatoms—*Ditylum brightwellii, Chaetoceros affinis, Thalassiosira decipiens,* and *Leptocylindrus danicus*; 2) dinoflagellates—*Gymnodinium splendens, Gonyaulax polyedra, Prorocentrum micans,* and *Peridinium trochoideum*; and 3) flagellates—*Chlamydomonas* sp. and *Dunaliella* sp.

Feeding trial no. (duration in hours)	Temp (°C)	Air-stone	Food organism	Concentration of food particles (organisms/ml)	Number of larvae per experiment	Feeding by anchovy larvae: % of larvae with ¼ to full gut	% of larvae with <8 particles in gut	% of larvae with empty gut
1 (7.25)	18.2		*G. splendens*	162	65	65	7	28
	18.2	X	*G. splendens*	162	54	48	9	43
	18.2	X	*G. splendens*	162	70	53	16	31
2 (8.0)	18.2		*G. splendens*	180	70	33	16	51
	18.5	X	*D. brightwellii*	164	59	0	0	100
	19.6	X	*D. brightwellii*	164	46	0	0	100
3 (8.0)	17.0		*G. splendens*	240	67	67	16	17
	17.0	X	*C. affinis*	127 chains	59	0	0	100
	17.0	X	*C. affinis*	127 chains	80	0	0	100
	17.0	X	*T. decipiens*	154	73	0	0	100
	17.0	X	*T. decipiens*	205	69	0	0	100
4 (8.0)	17.1		*G. splendens*	195	60	55	7	38
	16.9	X	*L. danicus*	197 chains	75	0	0	100
	16.9	X	*L. danicus*	780 chains	57	2	0	98
5 (8.0)	17.4		*G. splendens*	208	62	34	10	56
	17.7		*P. trochoideum*	56	65	67	22	11
	17.7		*P. trochoideum*	97	54	65	7	28
	17.7		*P. trochoideum*	210	46	50	26	24
	17.7		*Chlamydomonas* sp.	211	46	0	0	100
	17.7		*P. micans*	201	38	45	21	34
6 (8.0)	18.2		*G. splendens*	193	26	58	23	19
	18.2		*G. polyedra*	102	58	78	7	15
	18.2		*G. polyedra*	60	48	60	10	30
	17.7		*Dunaliella* sp.	303	67	0	0	100
	17.7		*Dunaliella* sp.	242	31	0	0	100

was provided for 14 h/day by 40-W fluorescent lamps as described earlier.

Eight rearing containers were inoculated with *G. splendens* and eight with *Gonyaulax polyedra* at a concentration of 100 organisms/ml. As a supplement to these food organisms, some containers were also stocked with a combination culture of the rotifer, *Brachionus plicatilis,* and the harpacticoid copepod, *Tisbe holothuriae,* with final concentrations of 0.0, 0.1, 1.0, and 5.0 organisms/ml (Table 3). Duplicate experiments were run simultaneously for all treatments including two containers without dinoflagellates but stocked with *B. plicatilis* and *T. holothuriae,* at a concentration of 5 organisms/ml.

The relative proportions of *B. plicatilis* and *T. holothuriae* (hereafter also referred to as microzooplankton) in the larval rearing containers

TABLE 3.—Survival and growth of anchovy larvae reared for 10 days on different diet regimes.

Stocking density of larvae on day 0 (no./liter)	Concentration of dinoflagellate (organisms/ml)	Concentration of microzooplankton (organisms/ml)	Survival: Number	Survival: Percent	Standard length (mm): Mean	Standard length (mm): S_x	Average weight (mg)
	Gymnodinium splendens						
3.3	100	5.0	11	33.3	4.24	0.359	0.039
3.4	100	5.0	15	44.1	4.87	0.671	0.048
2.2	100	1.0	5	22.7	4.30	0.480	0.061
2.5	100	1.0	12	48.0	4.73	0.677	0.047
3.1	100	0.1	13	41.9	4.46	0.355	0.046
3.9	100	0.1	6	15.4	3.57	0.314	0.046
2.8	100	0.0	9	32.1	4.23	0.485	0.042
3.6	100	0.0	8	22.2	4.03	0.413	0.056
	Gonyaulax polyedra						
3.3	100	5.0	5	15.2	4.02	0.403	0.065
3.9	100	5.0	14	35.9	4.82	0.710	0.059
3.8	100	1.0	5	13.2	4.54	0.796	0.077
3.7	100	1.0	7	18.9	4.41	0.219	0.057
2.8	100	0.1	1	3.6	3.7	—	(1)
2.9	100	0.1	1	3.5	4.0	—	(1)
3.5	100	0.0	1	2.9	3.0	—	(1)
3.9	100	0.0	0	0.0	—	—	—
4.2	0	5.0	8	19.1	4.51	0.669	0.050
2.3	0	5.0	0	0.0	—	—	—

[1] Sample too small to weigh.

varied during the course of the experiment. Initially, approximately 90% of the microzooplankters in the containers were *T. holothuriae*, but by the end of the rearing experiment, *B. plicatilis* was the dominant organism (97%). We were unable to determine if the anchovy larvae were selectively feeding on the copepods because the combination culture of microzooplankton which was used to stock the larval rearing containers also experienced a similar succession in species dominance during the experimental period.

Brachionus plicatilis and *T. holothuriae* were cultured together in the same vessel using techniques described by Hunter (1976). The cultures were filtered through 105-μm screening to remove the largest organisms before inoculating the larval rearing containers. Microscopic examination of the filtrate revealed a predominance of small rotifers and copepod nauplii.

Fifty anchovy eggs were added to each container the day after spawning and the appropriate dinoflagellate was also introduced at this time. Hatching occurred on the next day, which corresponds to day 0 of the experiment. The number of dead embryos on the container bottom was counted at this time and the percentage hatch was calculated. On day 2, most of the yolk sac was absorbed, the eyes were pigmented, and the larvae initiated feeding. At this time, the microzooplankton were added. The experiments were terminated on day 10; standard lengths were measured for each animal; average dry weight for larvae in each container was determined; and the percent survival in each container was calculated.

Each larval rearing container was sampled daily to monitor the concentration of food organisms. Because *Gymnodinium splendens* and *Gonyaulax polyedra* tend to form patches, 1-ml samples were taken from three different locations in the tank outside of a patch; the numbers were averaged and an appropriate amount of a dense dinoflagellate culture was added daily to maintain a concentration of 100 organisms/ml. The density of *B. plicatilis* and *T. holothuriae* was maintained in a like manner except that the volume sampled was larger (from 10- to 100-ml samples/container, depending on the stock density of microzooplankton). Also, we were careful to sample a few centimeters away from the container surfaces because *T. holothuriae* copepodids and adults are thigmotactic. We stocked the rearing containers with nauplii (which are less thigmotactic than the older stages). However, during the course of the experiments, surviving *T. holothuriae* developed beyond the naupliar stages and tended to settle out on container surfaces becoming less available to anchovy larvae. These stages were not included in our counts.

RESULTS

Feeding Experiments

A total of 518 larvae were presented with four species of diatoms (Table 2). Only one larva fed on diatoms. This single individual ate a narrow (5 × 50–75 μm) chain-forming diatom, *Leptocylindrus danicus*.

Most larvae fed on the dinoflagellates *Gymnodinium splendens*, *Gonyaulax polyedra*, *Prorocentrum micans*, and *Peridinium trochoideum*. There was no apparent preference by larvae for a particular species of dinoflagellate. Between 72 and 89% of the larvae tested fed on *P. trochoideum* (20 μm), which are as small as the smallest sized particles known to be ingested by first feeding anchovy larvae (Arthur 1976). *Peridinium trochoideum* is a darkly pigmented dinoflagellate. Perhaps this characteristic makes it more visible to the larvae than other particles of a similar size. Lasker (1975) concluded that first feeding anchovy larvae required a particle greater than 40 μm to fill their gut in 8 h.

Anchovy larvae did not feed on the smallest prey used in the feeding experiments, the flagellates *Chlamydomonas* sp. (10 μm) and *Dunaliella* sp. (6 μm).

Larval Rearing Experiments

Growth and survival of anchovy larvae reared for 10 days on different diet regimes are shown in Table 3. The survival rate of larvae reared on the *Gymnodinium splendens* diet was higher than on the *Gonyaulax polyedra* diet. The relationship between larval survival and supplementation of the dinoflagellate diet with microzooplankton was described with linear regressions (Figure 1). The survival of larvae reared in seawater containing 100 *Gymnodinium splendens*/ml did not significantly increase (t for the slope of the regression = 0.1, $P<0.20$) when microzooplankton were added to their diet as a supplement (Figure 1). Supplementation of the *Gonyaulax polyedra* diet with microzooplankton did result in a significant increase (t for the slope of the regression = 3.24,

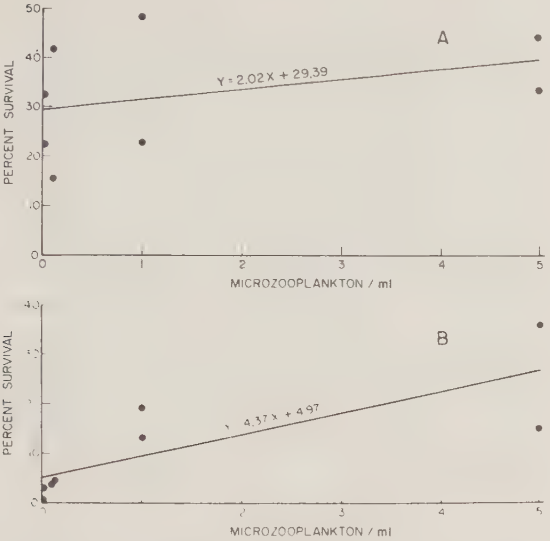

FIGURE 1.—Percent survival of *Engraulis mordax* at 10 days in relation to supplementation of a dinoflagellate diet with microzooplankton. A) *Gymnodinium splendens* diet. B) *Gonyaulax polyedra* diet.

$P < 0.025$) in larval survival. Larvae reared on a *G. polyedra* diet required at least 1 microzooplankton/ml in order to have survival rates that were comparable to larvae reared on a diet of *Gymnodinium splendens*. These results were comparable to the survival rates recorded by O'Connell and Raymond (1970) for anchovy larvae fed copepod nauplii at various concentrations. They found that larvae did not survive for 12 days in containers with less than 1 nauplius/ml.

Although anchovy larvae grow slowly during the first several days of feeding, a slight but significant increase ($t = 2.67$, $P < 0.05$) in standard length occurred in larvae fed *G. splendens* when their diets were supplemented with microzooplankton (Figure 2), but no differences in dry weight were detected. Larvae fed *Gonyaulax polyedra* also appeared to increase in standard length when their diets were supplemented (Figure 2), but because the increase was slight and the number of data points was small due to the low survival rates on this diet, no significant increase was detected ($t = 1.50$, $P > 0.20$).

Survival was low in larvae fed only 5 microzooplankters/ml without any dinoflagellates (Table 3). One container had no survivors and the other had 19.9% survival. Theilacker and McMaster (1971) found that larval anchovies that were fed only rotifers (*B. plicatilis*) had a lower

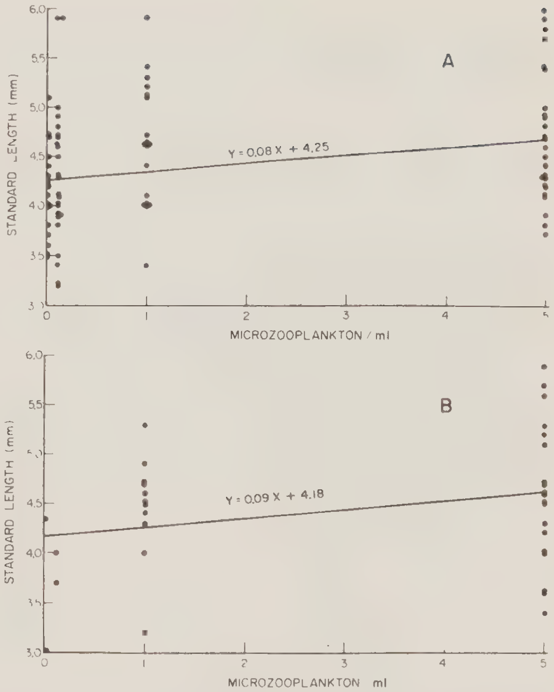

FIGURE 2.—Standard lengths of *Engraulis mordax* at 10 days in relation to supplementation of a dinoflagellate diet with microzooplankton. A) *Gymnodinium splendens* diet. B) *Gonyaulax polyedra* diet.

rate of survival than those fed *Gymnodinium splendens* and *B. plicatilis* in combination. They related this finding to the low feeding success of larvae on the larger sized rotifers during the first few days of feeding. Also, Houde (1973) believes that survival of fish larvae is increased when blooms of phytoplankton are maintained in rearing containers to "condition" the water (presumably by removing metabolites).

DISCUSSION

Anchovy larvae apear to select their prey and it seems as if size is not the only criterion for selection. Larvae did not feed on any of the four species of diatoms tested in this study. The most obvious explanation is that spines and other processes on the diatoms either discouraged the larvae from striking or prevented them from swallowing. On the other hand, most larvae fed on all species of dinoflagellates tested. Visibility might also play an important role in prey selection since the darkly pigmented dinoflagellate, *P. trochoideum*, was heavily preyed upon by anchovy larvae even though *P. trochoideum* are as small as the smallest particles detected by Arthur (1976) in the guts of larval anchovies.

It appears that prey differ in their nutritional value to anchovy larvae. *Gymnodinium splendens* and *Gonyaulax polyedra* are readily eaten by anchovy larvae, but *G. polyedra* was an inadequate food. Only 1 larva of the 74 that were reared on an exclusive diet of *G. polyedra* survived for 10 days. Larvae reared on a diet of *G. polyedra* supplemented with microzooplankton had survival rates that increased relative to the degree of supplementation. Although certain species of *Gonyaulax* are known to be toxic, it seems unlikely that this was a cause of mortality in our experiments because survival was good when larvae were fed *G. polyedra* supplemented with 5 microzooplankters/ml.

We offer two possible explanations for the difference in the nutritional value of the two dinoflagellates: 1) *G. polyedra* is about 10 μm smaller in diameter than *G. splendens*. Therefore, on the basis of volume alone, *G. splendens* could have twice as many calories as *Gonyaulax polyedra*, because the volume increases as the cube of the radius in a sphere. 2) *G. polyedra* is armored while *Gymnodinium splendens* is not, and, therefore, *G. splendens* is presumably more digestible by anchovy larvae which have an undifferentiated gut during the early stages of their development. Lasker et al. (1970) found that the armored dinoflagellate, *Prorocentrum micans* (27 × 38 μm), did not sustain life in first feeding anchovy larvae but again, this organism is smaller than *G. splendens*.

Lasker (1975) concluded that the nearshore area of the Southern California Bight was a good feeding ground for first feeding anchovy larvae during the spring of 1974 because of the high concentrations of *G. splendens* found in the chlorophyll maximum layer. In this study, the survival of anchovy larvae fed 100 *G. splendens*/ml was acceptable, and it did not differ from that of larvae fed a *G. splendens* diet supplemented with microzooplankton at concentrations up to 5 organisms/ml. Although larvae grew slightly faster when given the microzooplankton, these results still indicate that a larva could survive until an age of 10 days without the high concentrations of micronauplii that O'Connell and Raymond (1970) found to be necessary. If anchovy larvae survive to a size of 5 to 6 mm on *G. splendens*, their feeding efficiency would be higher than smaller larvae (Hunter 1972), and because of their larger size, the volume of water that larvae could search for food would also be increased. These factors would reduce the concentration of microzooplankton necessary for survival (Vlymen in press).

During several sampling periods in 1975, Lasker (in press) found that the chlorophyll maximum layer in the nearshore region of the Southern California Bight was dominated by *Gonyaulax polyedra* or a variety of small diatoms. Our work indicates that during the time periods when these phytoplankters predominated, feeding conditions for post yolk-sac anchovy larvae would be less suitable than when *G. splendens* was abundant.

ACKNOWLEDGMENTS

We thank James Alexander and Geoffrey Lewis for their technical assistance and Charles Bary for culturing the phytoplankton. Thanks also go to Reuben Lasker and John Hunter for reviewing the manuscript. This research was supported by a grant to Reuben Lasker from the Brookhaven National Laboratory.

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KOKO HEAD, OAHU, SEA-SURFACE TEMPERATURES AND SALINITIES, 1956–73, AND CHRISTMAS ISLAND SEA-SURFACE TEMPERATURES, 1954–73

GUNTER R. SECKEL[1] AND MARIAN Y. Y. YONG[2]

ABSTRACT

Sea-surface temperatures and salinities have been collected twice weekly at Koko Head, Oahu, Hawaii, since 1956; and at Christmas Island in the central equatorial Pacific, sea-surface temperatures have been collected daily since 1954. In 1971, Seckel and Yong used harmonic analysis as a curve-fitting method to bring these observations, 1 yr at a time, through 1969, into a form useful for descriptive and numerical applications. In this paper the analyses are updated through 1973 and the method is used to describe the entire data series.

The data series have been separated into several scales of variability: long-term variability (periodicities larger than 1 yr), short-term variability (12-mo and shorter periodicities), average annual cycle (the 12-, 6-, 4-, and 3-mo periods), and the residual variability that characterizes individual years (the short-term variability with the annual cycle removed). In contrast to the Koko Head temperature where the annual cycle predominates, the interannual variability predominates, at times obscuring the annual cycle, in the Koko Head salinity and Christmas Island temperature. The interannual change of the Koko Head salinity can be about three times, and that of the Christmas Island temperature can be about four times the average annual variability. In the average annual temperature and salinity cycles at Koko Head the amplitudes of the 6-, 4-, and 3-mo periods are small in relation to the 12-mo period. In the average annual temperature cycle at Christmas Island, however, the amplitude of the 6-mo period is almost one-half that of the 12-mo period. The residual variations exhibit changing amplitudes and periodicities at intervals of more than 1 yr that resemble amplitude and frequency modulations.

Speculations are made about processes that contribute to the temperature and salinity variations. It appears that in addition to the heat exchange across the sea surface, advection contributes materially to the observed changes at Koko Head and Christmas Island.

Harmonic coefficients resulting from the analyses are listed in the appendices to facilitate reproduction of the data presented.

In an earlier paper, Seckel and Yong (1971) used harmonic analysis as a curve-fitting method, bringing rapidly into usable form regularly sampled sea-surface temperatures and salinities. Analyses were made of sea-surface temperature and salinity obtained once or twice weekly from 1956 to 1969 at Koko Head, Oahu (lat. 21°16′N, long. 157°41′W,), and of sea-surface temperature obtained daily from 1954 to 1969 at Christmas Island (lat. 1°51′N, long. 157°23′W). The temperature and salinity variations for each year were then specified by sets of harmonic coefficients and phase angles. Values calculated at 15-day intervals from the resulting annual functions were used in long-term analyses of the entire data records. These analyses showed that interyear differences in the Koko Head salinity and Christmas Island temperature were larger than seasonal changes.

The long-term changes in surface properties reflect climatic scale ocean-atmosphere processes and, in turn, affect these processes. The changes in properties and processes affect life in the sea. For example, the Koko Head salinity changes indicate primarily changes in the advection produced by variations in ocean circulation (Seckel 1962). It was postulated that changes in circulation also affect the concentration and, therefore, the availability of skipjack tuna caught in Hawaii (Seckel 1972).

The long-term changes in the Christmas Island temperatures are linked with large-scale (at least ocean-wide) ocean-atmosphere processes. Bjerknes (1969) related anomalously high tem-

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Manuscript accepted March 1977.
FISHERY BULLETIN: VOL. 75, NO. 4, 1977.

peratures and high precipitation at Canton Island in the central equatorial Pacific with intensification of the Hadley circulation and changes in the "southern oscillation." Quinn (1974) related an index of the southern oscillation (the difference of atmospheric pressure between Easter Island and Darwin, Australia) with El Niño phenomena and abnormally high rainfall in the equatorial Pacific. One of the latter is the failure of the Peruvian anchovy fishery. The large interyear differences of equatorial sea-surface temperatures undoubtedly affect the biota in as yet undescribed ways.

It is of value, therefore, to bring the results of monitoring into a form that is useful for fishery applications. Toward this objective we have 1) updated our previous Koko Head and Christmas Island analyses through 1973; 2) analyzed the long series (18 yr for Koko Head, 20 yr for Christmas Island) and separated changes into long-term variability, the annual cycle, and the short-term variability that characterizes individual years; and 3) speculated about the processes that affect the changes evident in the data records.

THE 1970-73 UPDATE

Sampling and Processing

Koko Head, where bucket samples for temperature and salinity determinations were taken twice weekly, is located at the exposed, eastern shore of Oahu. At this location, cliffs extend into the water, and temperature and salinity samples have been found to be representative of offshore conditions. At Christmas Island, bucket temperatures were obtained daily near the plantation village on the ocean side of the lagoon entrance. Measurements were made during the morning at each location.

The procedures used to derive the harmonic coefficients for the 1970-73 observations were the same as those described by Seckel and Yong (1971). Fourier analysis was performed on the residuals from a linear fit so that the temperatures and salinities are expressed as a function of time, t, by

$$S = K + bt + \sum_{n=1}^{k} C_n \cos \omega (nt - \alpha_n) \ldots \qquad (1)$$

where $K = F(t_0) + \frac{A_0}{2}$, $\omega = \frac{2\pi}{T}$, and k is the highest harmonic in the series. $F(t_0)$ is the first observed value, A_0 is the Fourier coefficient for $n = 0$, C_n are the coefficients for $n \neq 0$, and α_n are the phase angles. b is the slope of the straight line joining the first and last observations of the fundamental period, T.

The fundamental period for the Koko Head analyses was 365 days. For the Christmas Island analyses the fundamental periods were 120 which for a full year followed in sequence with a 30-day overlap from Julian day 1 to 20, 91 to 210, 181 to 300, and 271 to 390 extending 25 days into the following year.

Results

Results of the analyses for the update years are presented in the appendices. Coefficients and phase angles for the Koko Head temperatures and salinities are found in Appendix A, Tables 1 and 2. Figures of the expected values computed from the harmonic functions together with the observed values for the Koko Head temperatures and salinities are found in Appendix B, Figures 1 and 2. The coefficients and phase angles for the Christmas Island temperatures are found in Appendix C, and the plotted functions together with the observed values are found in Appendix D.

Standard errors of estimate for the fitted Koko Head temperatures and salinities and Christmas Island temperatures are listed in Appendix E, Tables 1, 2, and 3, respectively.

Christmas Island Data Problems

Observer problems at Christmas Island caused the sea temperature sampling to be interrupted from May 1972 to April 1973. The data gap was reduced by Hawaii Institute of Geophysics (HIG) bucket temperatures obtained daily since November 1972 near the airport on the northeast shore of the island. Although NMFS (National Marine Fisheries Service) sampling resumed in April 1973, HIG data were used in our analysis for the entire year. In our long-term analysis the remaining data gap between May and November 1972 was closed by linear interpolation. Mean monthly temperatures obtained from the two sampling sites indicate that NMFS temperatures are on average about 0.5°C lower than the HIG values (Table 1). The HIG data have not been adjusted to reflect this temperature difference.

The large scatter of data at Christmas Island

TABLE 1.—Mean monthly sea-surface temperature (°C), Christmas Island: National Marine Fisheries Service station (NMFS) and Hawaii Institute of Geophysics station (HIG).

	Date	NMFS	HIG
1973	May	26.6	26.2
	June	24.7	25.6
	July	23.6	25.2
	August	23.9	24.5
	September	23.8	24.1
	October	23.4	23.8
	November	23.0	23.3
	December	23.4	23.5
1974	January	23.9	24.0
	February	24.1	24.3
	March	24.6	24.7
	April	24.7	25.2
	May	23.9	24.9
	June	23.6	25.0
	Average	24.1	24.6

in comparison with that at Koko Head indicates another data problem. The scatter probably is caused by sampling of water in the shallow beach area that is more sensitive to changes in the local heating-cooling processes than the deep water of an offshore site.

Finally, there are no systematically observed sea-surface temperatures near Christmas Island against which the shore measurements can be calibrated. However, the monthly pamphlet *Fishing Information*[3] contains a temperature chart for the equatorial Pacific. Contours near Christmas Island are based on insufficient observations to reproduce the temperature distribution reliably. Therefore, the values from these charts, plotted on the annual graphs of Appendix D, show large variations in the difference between the *Fishing Information* temperatures and Christmas Island observations. On average the *Fishing Information* values are 1.3°C higher than the midmonth expected values with differences ranging from −1.2° to 4.1°C.

The discrepancy between the temperature sets, in part, may be due to a tendency toward a warm bias of merchant vessel temperature reports. More probable, however, Christmas Island temperatures, being measured in the morning, reflect the effect of night cooling in shallow water that would be in excess of the temperature decline taking place in deeper, offshore water.

Despite the apparent discrepancies between the beach and offshore temperatures, the data from the shore sampling sites reflect climatic scale anomalies. For example, both the Christmas Island record (Seckel and Yong 1971) and the Canton Island record (Bjerknes 1969) show the equatorial cold anomaly of 1955-56, the warm anomaly of 1957-58, and the anomalous biannual temperature variations of 1963-67.

ANALYSES OF LONG-TERM DATA RECORDS

In this section we present harmonic analysis results of the entire data series and separately display the long-term variability, the short-term variability, the average annual cycle, and the variability that characterizes individual years.

The entire data series is expressed by the function

$$S_L = A + \sum_{n-1}^{k} C_n \cos \omega (nt - \alpha_n) \ldots \qquad (2)$$

where A gives the average value of the series, k is the highest harmonic of the analysis, and other symbols have the same meaning as given for Equation (1).

Input values for these analyses were calculated at 15-day intervals from the annual analyses presented in this and our previous paper (Seckel and Yong 1971). Analysis of the 1956-73 Koko Head data was carried to the 72d harmonic and of the 1954-73 Christmas Island data to the 80th harmonic so that the shortest period resolved in each series is 3 mo. Analyses were carried out on the residuals from a linear fit as in the analyses of the annual data sets. The harmonic and linear coefficients for the long-term series are listed in Tables 1, 2, and 3 of Appendix F.

The fitted curves resulting from these analyses together with the input values are shown in panels A of Figures 1, 2, and 3. Dominant in the Koko Head temperature is the annual variation without pronounced longer term trends other than the rise of maximum and minimum temperatures from 1966 to 1968. In contrast to the Koko Head temperature curve, the salinity curve shows longer term variations that are larger than the seasonal variations. Also, during some years such as in 1957, annual variation is not apparent. The Christmas Island temperatures convey a similar picture; interannual changes are larger than the annual changes. Again, the latter may be obscured or absent as during the years 1963-66 and in 1973 when biannual changes dominated.

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[3] *Fishing Information*. March 1970 through December 1973. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Southwest Fish. Cent., La Jolla, Calif.

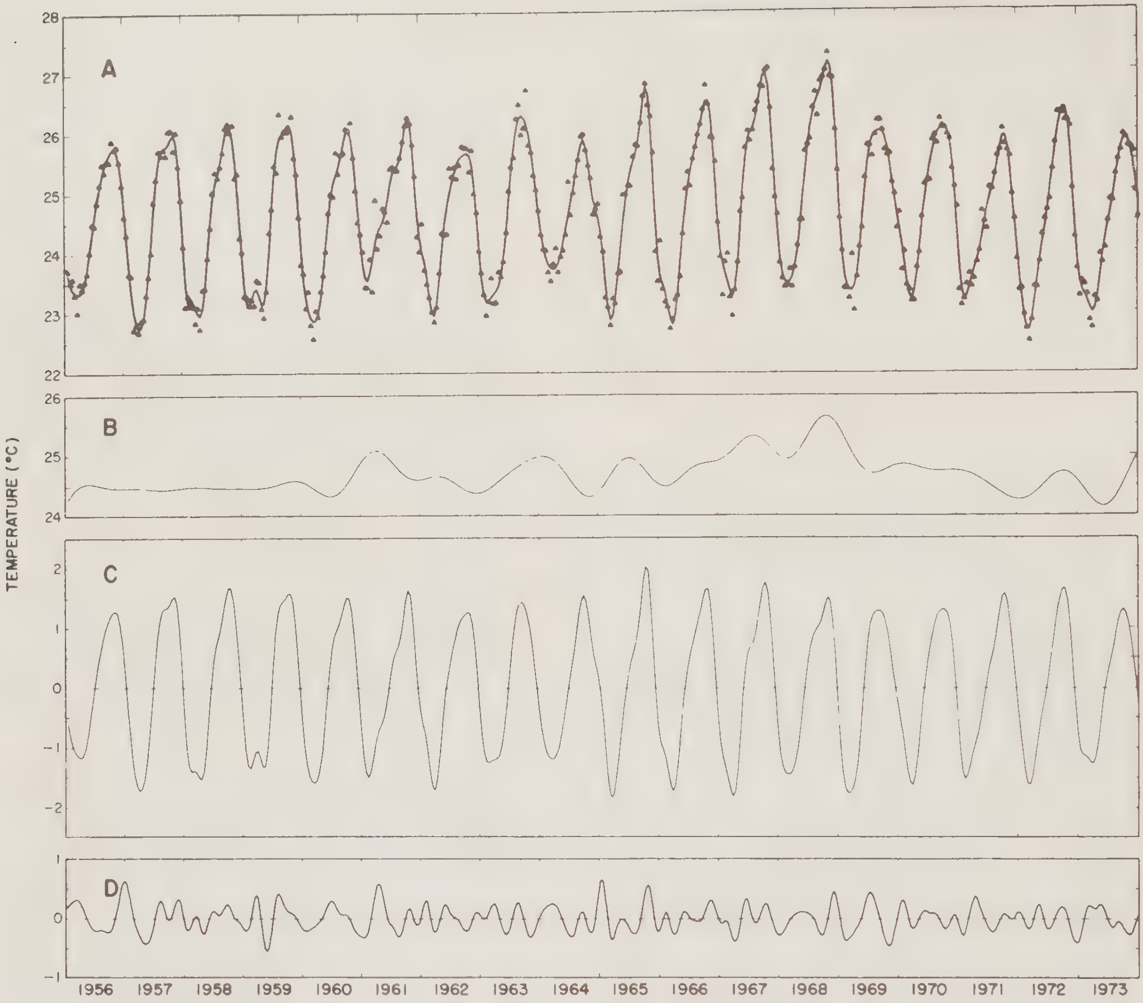

FIGURE 1.—Koko Head temperature, 1956-73: A. Fitted curve with a 3-mo resolution (n = 1-72). B. Long-term variation (n = 1-17). C. Short-term variation (n = 18-72). D. Residual variation (n = 19-35, 37-53, 55-71).

The amplitudes (C_n) of the long-term analyses (Figure 4) confirm these qualitative impressions. In the Koko Head temperature, the amplitude of the annual sinusoid (18th harmonic) is dominant and almost six times as large as the largest amplitude of the long periods. In the Koko Head salinity and Christmas Island temperature, on the other hand, long periods have the largest amplitudes. For the Koko Head salinity the amplitude of the fourth harmonic is larger than that of the annual sinusoid and for the Christmas Island temperature the amplitude of the first harmonic is almost twice that of the annual sinusoid.

Long-Term Changes

When long-term changes are of interest, the annual and shorter term variability can be filtered by a variety of methods including the commonly used 12-mo moving average method. After harmonic analysis has been used as a curve-fitting technique, however, it is simple to evaluate only the terms in the harmonic function up to but not including the annual sinusoid in order to display long-term changes. Thus, in Equation (2), the Koko Head temperatures and salinities were evaluated for n = 1 to 17 and the Christmas Island temperatures for n = 1 to 19. The resulting

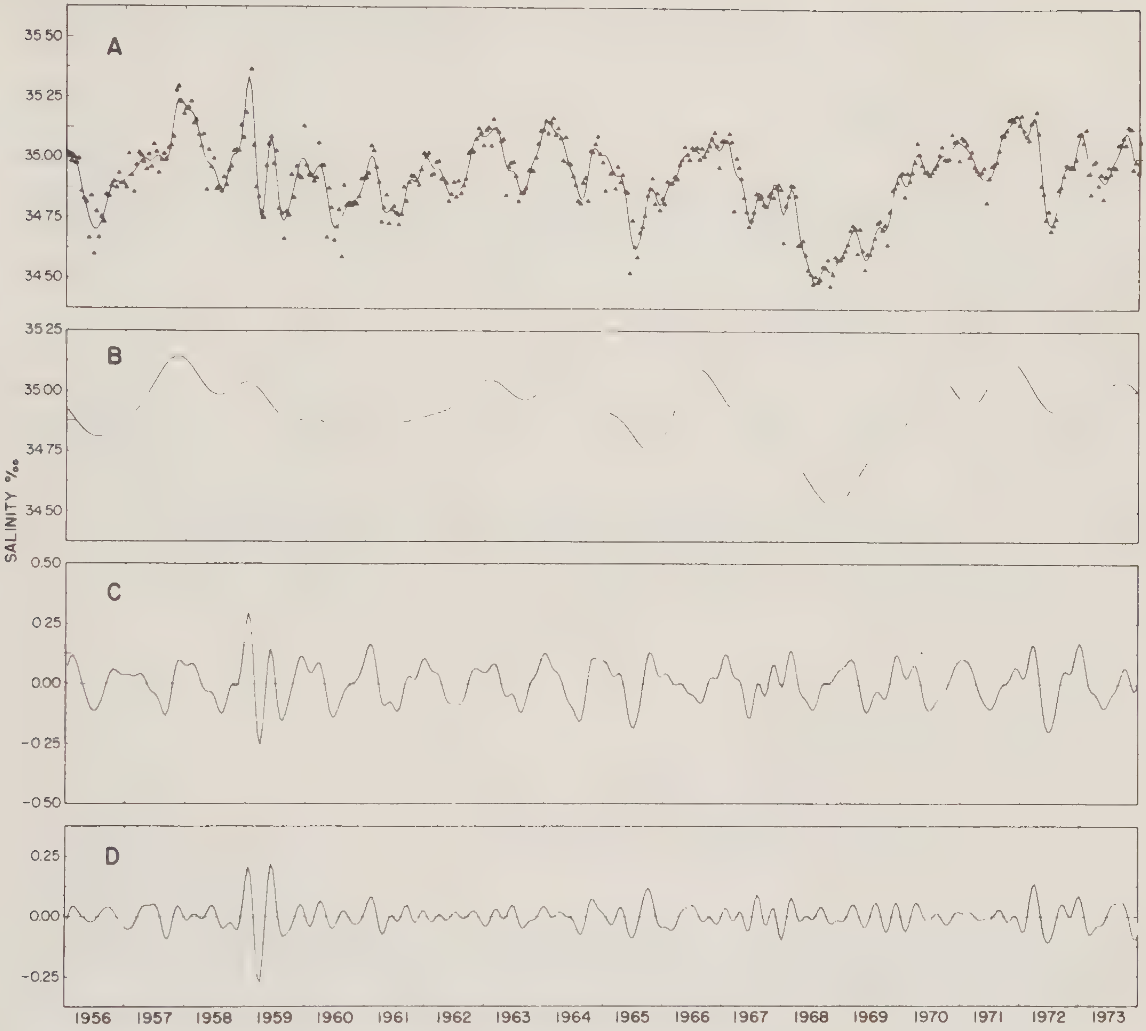

FIGURE 2.—Koko Head salinity, 1956-73: A. Fitted curve with a 3-mo resolution (n = 1-72). B. Long-term variation (n = 1-17). C. Short-term variation (n 18-72). D. Residual variation (n = 19-35, 37-53, 55-71).

curves are shown in panels B of Figures 1, 2, and 3.

In the Koko Head temperature little variation due to the longer period harmonics is apparent until 1960 when perturbations of 0.5° to 1°C began. A rising temperature trend between 1966 and 1968 was followed by a decline to a pre-1960 temperature level. Both the Koko Head salinity and Christmas Island temperatures show the large perturbations previously noted. At Koko Head a pronounced salinity decline began in 1966, reaching almost 34.5‰ in 1968 before rising again to a range near 35‰. Times of high Christmas Island temperatures stand out. A prominent feature is the pronounced temperature decline during 1973 from one of the highest values to the coldest temperatures observed during the 20 yr of our record.

Short-Term Changes

The short-term changes relative to the long-term trends are another scale of interest that can be obtained by subtracting the moving average or the long-term values of the previous section from the monthly observations. In our case, and

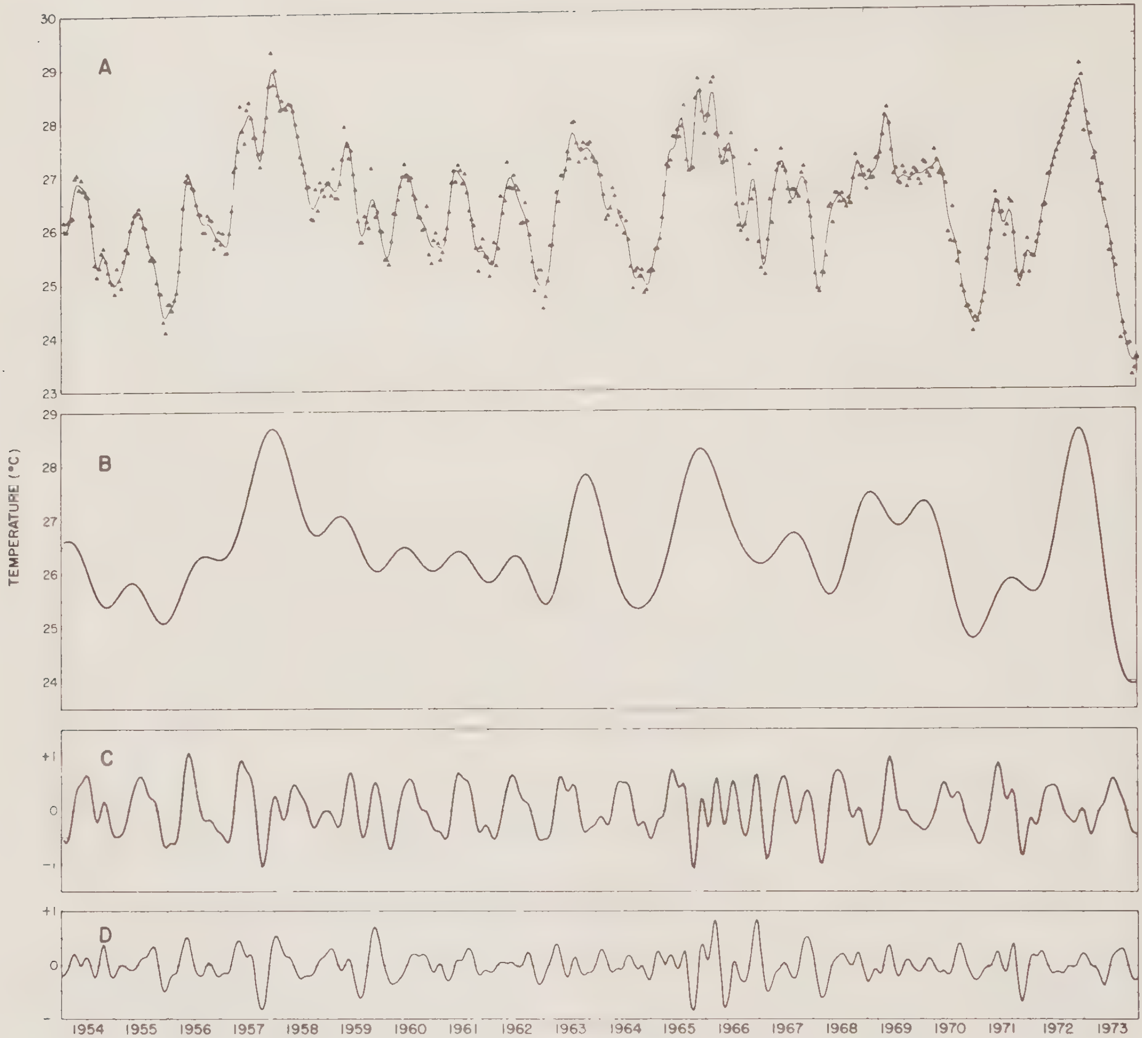

FIGURE 3.—Christmas Island temperature, 1954-73: A. Fitted curve with a 3-mo resolution (n = 1-80). B. Long-term variation (n = 1-19). C. Short-term variation (n = 20-80). D. Residual variation (n = 21-39, 41-59, 61-79).

when variations of <3 mo need not be resolved, it is simple to display short-term changes by evaluating the higher harmonics in Equation (2) beginning with the annual sinusoid (n = 18-72 for Koko Head, n = 20-80 for Christmas Island). The resulting curves are shown in panels C of Figures 1, 2, and 3.

The Koko Head temperature curve looks similar to the initial harmonic fit (Figure 1A) because the long-term changes are small in comparison to the annual variations. In the case of the Koko Head salinity and the Christmas Island temperature, the annual variations that during some years were obscured by the long-term trends are clearly apparent. At Koko Head low salinities occur during spring and summer and high salinities during fall and winter. At Christmas Island high temperatures occur in late spring and low temperatures in fall or winter.

Annual Sinusoid and Its Harmonics

Evaluation of the annual sinusoid and its harmonics yields the mean annual variation. For annual analyses the harmonics n = 1, 2, 3, and 4 have periods of 12, 6, 4, and 3 mo. For the 18-yr

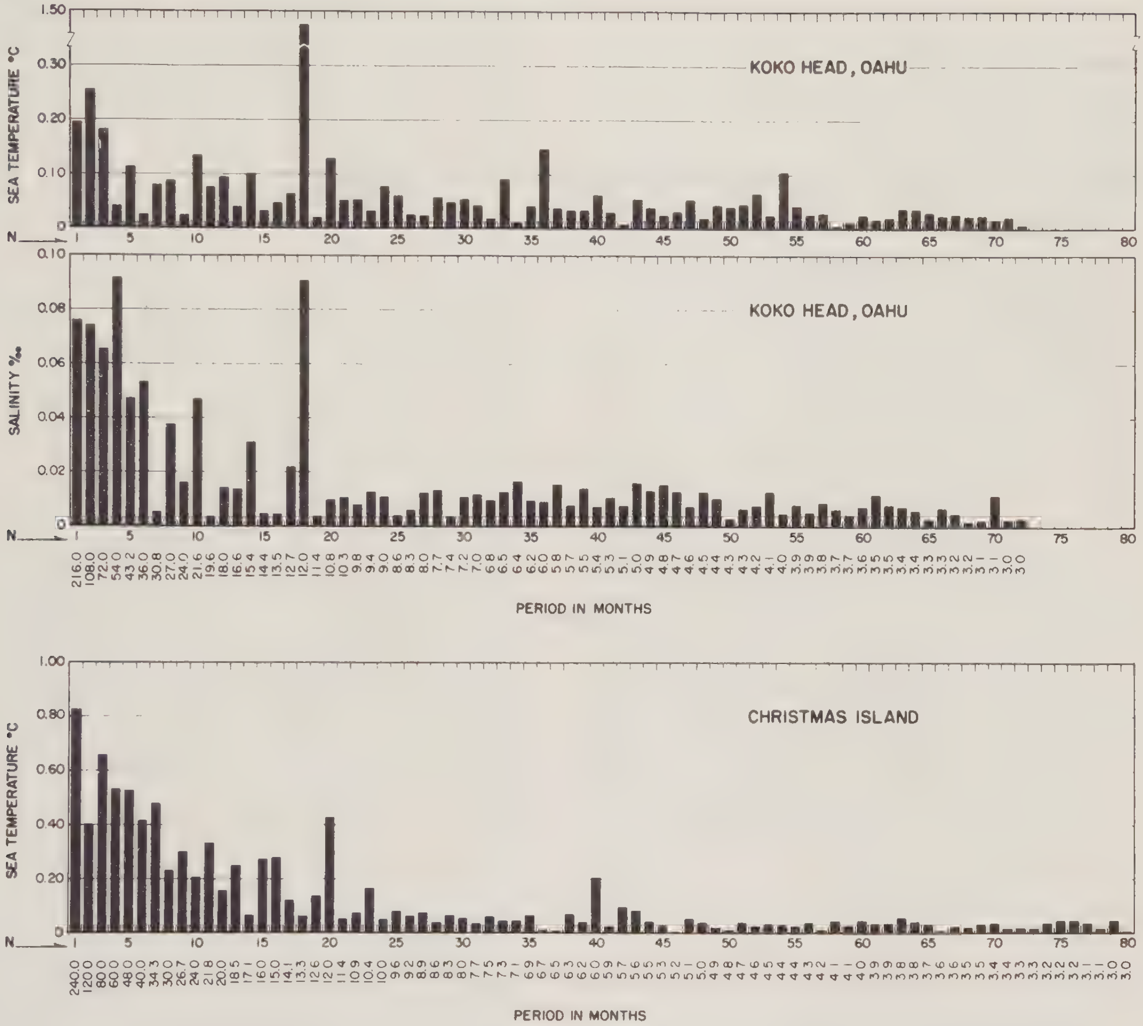

FIGURE 4.—Absolute magnitude of amplitudes of the long-term harmonic functions for Koko Head temperatures, 1956-73; Koko Head salinities, 1956-73; and Christmas Island temperatures, 1954-73.

Koko Head series, these periods are given by $n = 18, 36, 54$, and 72; and for the 20-yr Christmas Island series, they are given by $n = 20, 40, 60$, and 80. The mean annual variations evaluated from Equation (2) are shown in Figure 5 panels A, B, and C.

The mean annual temperature range of 3°C at Koko Head is about twice the long-term range. In contrast, the mean annual salinity range is 0.2‰ and only about 30% of the long-term range. At Christmas Island the mean annual temperature range is 1°C and only one-quarter of the long-term range.

At Koko Head the annual sinusoid, although visibly modified, dominates the mean annual changes. In both the temperature and the salinity, the amplitude of the annual sinusoid is an order of magnitude larger than that of the 6-, 4-, and 3-mo sinusoids (Figure 4). In the case of the temperature, the interference pattern of the 6- and 4-mo sinusoids is such that during the first half of the year the annual sinusoid is not visibly affected. Constructive interference by these sinusoids depresses the annual sinusoid by about 0.2°C in August, which causes first an increase by that amount in October and then a decrease by the end

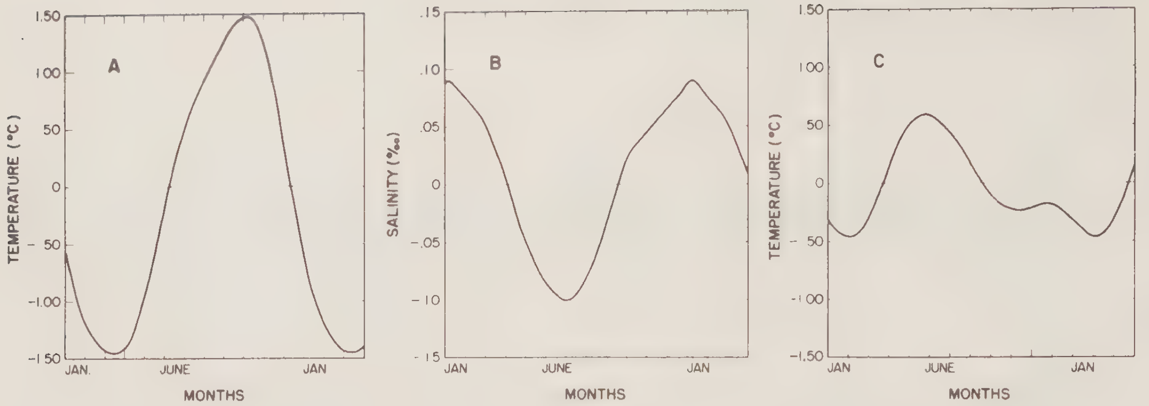

FIGURE 5.—Mean annual variations: A. Koko Head temperatures (n = 18, 36, 54, 72). B. Koko Head salinities (n = 18, 36, 54, 72). C. Christmas Island temperatures (n = 20, 40, 60, 80).

of the year. Consequently, the mean annual curve reflects the temperature trends evident in individual years in that warming lasts between 1 and 2 mo longer than cooling and the cooling rate is higher than the warming rate.

Departures of the mean annual salinity variation from the annual sinusoid, evident in Figure 5B, are not significant.

In contrast to the Koko Head spectra, the amplitude of the 6-mo sinusoid at Christmas Island is large enough to produce a significant modification of the annual sinusoid (Figure 5C). The absolute amplitudes of the 12-, 6-, 4-, and 3-mo sinusoids are 0.43°, 0.21°, 0.04°, and 0.003°C, respectively. Thus, the mean annual temperature variation at Christmas Island has the typical interference pattern produced by a 12- and a 6-mo sinusoid as illustrated in Figure 6. The residual curve, namely the difference between the mean annual curve and the annual sinusoid, is approximately the 6-mo sinusoid.

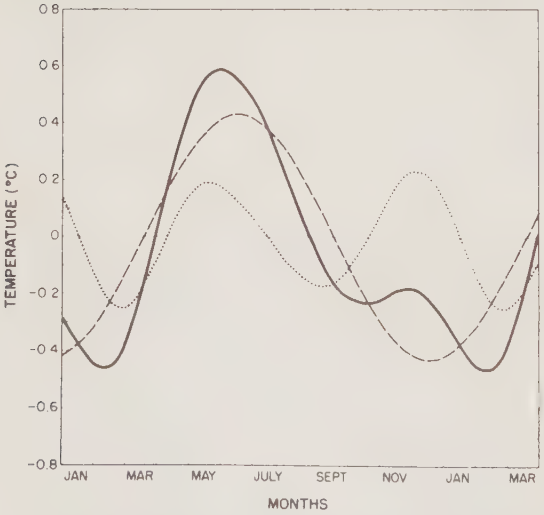

FIGURE 6.—Interference patterns of sinusoids for mean annual variation at Christmas Island. Solid line – n = 20, 40, 60, 80; dashed line – annual sinusoid (n = 20); dotted line – remaining variation (n = 40, 60, 80).

Residual Variations

The dominant feature in the short-term curves (panel C of Figures 1, 2, 3) is the annual variation superimposed upon which is the variability that characterizes each year. This "residual" variability is obtained by evaluating in Equation (2) the short-term variability without the annual sinusoid and its harmonics (n = 19-35, 37-53, and 55-71 for Koko Head, and n = 21-39, 41-59, and 61-79 for Christmas Island). Residual variability is shown in panel D of Figures 1, 2, and 3.

The residual curves are the interference pattern produced by all the sinusoids used in the evaluation. The irregular amplitudes and periodicities occurring at intervals of more than 1 yr give an impression of amplitude and frequency modulations. For example, in the Koko Head salinity curve, relatively large perturbations occur in groups during 1959, 1964-65, 1967-68, 1969-70, and 1972-73. In the Christmas Island residual temperature curve, relatively large perturbations during 1955-60 are followed by smaller perturbations during 1960-65 and by larger perturbations again during 1965-68. These modulations are of a long-term nature but do not appear to be related with the variations shown in panel B of Figures 1, 2, and 3.

On the Separation of Variability Into Various Time Scales

Although there are a number of curve-fitting procedures such as were reviewed by Holloway (1958), we have found Fourier analysis to be a convenient method for the Koko Head and Christmas Island time series. The filtering described above is a byproduct of this method and serves interpretive and descriptive purposes.

Although the moving average method is not recommended for climatological time series,[4] it is commonly used. For this reason, curves obtained by the moving average and the harmonic analysis methods are compared in Figures 7 and 8. The long-term as well as the residual curves of the two procedures are similar though not identical. The amplitudes of the long-term variations are larger in the curves derived by harmonic analysis than in those derived by the moving average method. This difference is to be expected because, in contrast to the harmonic method, input values in the moving average method are weighted equally.

The examples in Figures 7 and 8 were chosen because they illustrate limitations, in terms of physical interpretations, of the filtering techniques. A time series of the sea-surface temperature (salinity) is the signature of processes that govern the observed changes. What information about the governing processes, then, can be inferred from the time series? For example, is the observed change of temperature the result of an anomaly in the local heat exchange across the sea surface and advection produced by the local wind driven current, or is this temperature change a part of a larger scale change with the local processes remaining normal? The examples in panel B of Figures 7 and 8 exhibit variations with an annual periodicity during 1957 in the Koko Head salinity and during 1963, 1964, and 1965 in the Christmas Island temperature although this periodicity is not apparent in panel A of Figures 2 and 3. In these cases were annual variations, such as produced by annually varying processes, present or were they absent?

In the case of the moving average method, 2 yr of data are required to provide the smoothed curve for a single year. At Koko Head the normal midyear declines in salinity occurred during 1956 and 1958, affecting the shape of the smoothed 1957 curve. Consequently the residual curve showed an annual variation during 1957 (Figure 7B). At Christmas Island (Figure 8B), the residual temperature curve during 1964 also exhibits an annual variation, a maximum in spring and a minimum in fall, although no seasonal trends were indicated during the adjacent years (Figure 3A). In this case, was the normal annual variation in temperature present but obscured by the long-term trend?

In the harmonic analysis procedure the dominant signal in the annual variation is produced by the annual sinusoid. The amplitude of this period is determined by all the data in the series and contributes the same amount to the short-term variations of every year shown in panel C of Figures 1, 2, and 3. For example, a time series could be synthesized by combining a long-term variation with one that has an annual periodicity

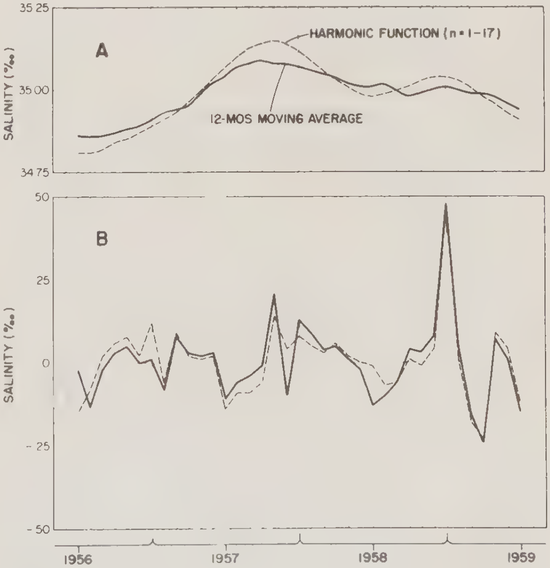

FIGURE 7.—Koko Head salinity, 1956-59: A. Long-term variation produced by 12-mo moving average and by harmonic function (n = 1-17). B. Short-term variation (monthly input values minus long-term values). Solid line — 12-mo moving average; dashed line — harmonic function (n = 1-17).

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[4] Climate change. Tech. Note 79, WMO-No. 195, Tp. 100. Secr. World Meteorol. Organ., Geneva, Switz., 1966, 79 p.

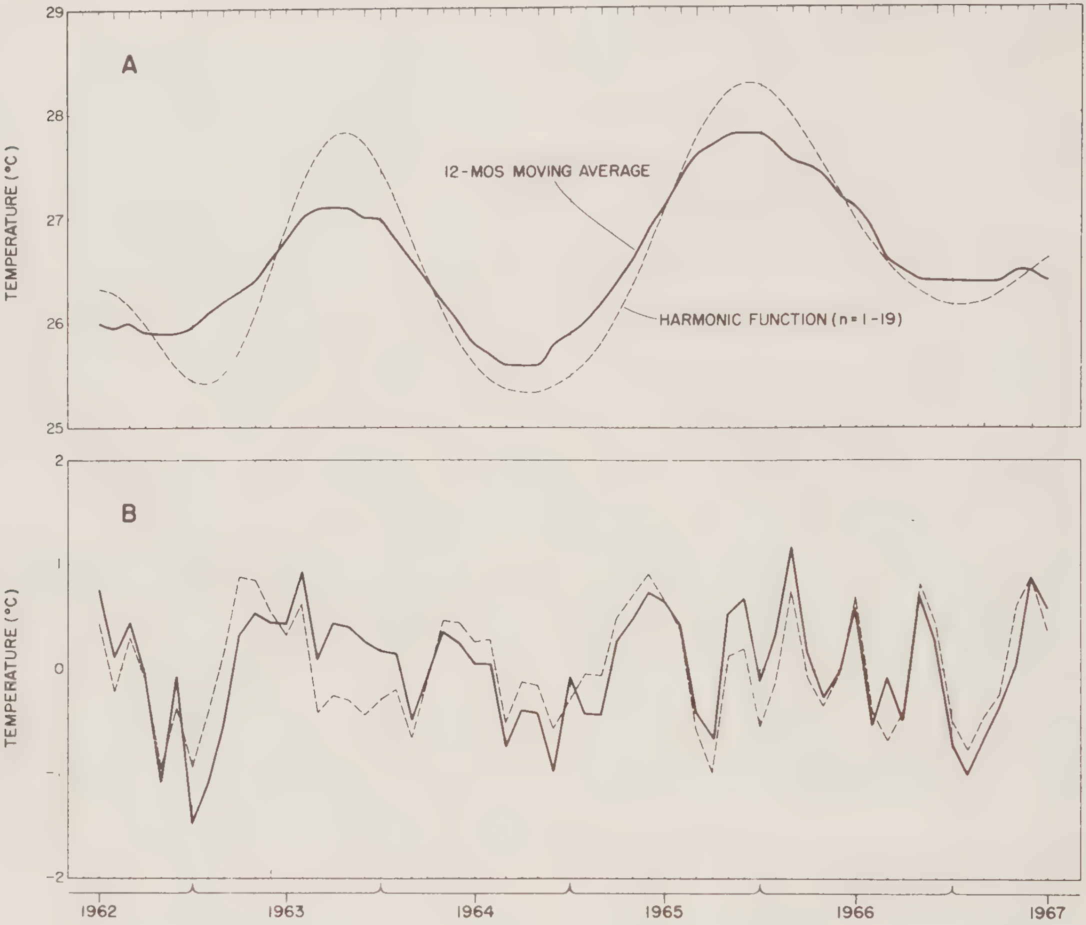

FIGURE 8.—Christmas Island temperature, 1962-67: A. Long-term variation produced by 12-mo moving average and by harmonic function (n = 1-19). B. Short-term variation (monthly input values minus long-term values). Solid line — 12-mo moving average; dashed line — harmonic function (n = 1-19).

every second year. After harmonic analysis and separating the hypothetical curve into a long-term and a short-term variation, the latter would exhibit an annual periodicity during every year.

Thus, the mathematical procedure cannot answer the questions posed above. The procedures illustrated in Figures 7 and 8 as well as other procedures, separate the scales of variability but there is no basis for inferring that the long-term changes are related with, possibly, ocean-wide processes and short-term changes with local processes. Only if the local processes are measured is there a physical basis for the separation into different scales of change.

Speculations About Temperature and Salinity Variations

It is not the purpose of this paper, and the information is not available, to investigate the causes for the temperature and salinity variations that have been described. Nevertheless, such an investigation would further an understanding of the fishery environment as well as the ocean-atmosphere linkages. It is useful, therefore, to speculate about the processes affecting changes in surface properties.

In Hawaiian waters air-sea interaction processes and advection appear to dominate the local change of temperature and salinity (Murphy et al. 1960; Seckel 1960, 1962). Advection is the product of the surface temperature (salinity) gradient and the component of the current normal to the isotherm or salinity isopleth. Generally near Hawaii the temperature increases and the salinity decreases equatorward. Consequently, with a northward component of flow, advection would increase the temperature and decrease the salinity at Koko Head.

The usual spring salinity decline at Koko Head is best explained by advection. It is estimated that at the latitude of Hawaii there is an excess of evaporation over precipitation with the highest excess occurring during spring and summer (Seckel 1962). Thus, since the salinity is increasing with depth, the only source of lower salinity water lies south of the islands.

On average the orientation of isotherms is northwest-southeast and that of salinity isopleth is zonal. In this case only the meridional component of flow causes salt advection, but both meridional and zonal components of flow cause heat advection. Consequently, meridional components of flow causing salinity variations do not necessarily produce temperature variations. Coincident changes of salinity and temperature that appear to be advection related, tend to occur during late winter and early spring when the North Equatorial Current is weak. For example, between days 60 and 110 of 1973 (Appendix B), decreasing and increasing temperatures corresponded with increasing and decreasing salinities. Pronounced coincident temperature and salinity variations occurred during the first half of 1959 and are most evident in the residual curves, panel D of Figures 1 and 2.

Coincident changes in temperature and salinity during specific seasons are not necessarily associated in the longer term. From 1956 through 1959 when the long-term salinity variations were pronounced, there was no long-term temperature change (panel B of Figures 1, 2). Later, a strong salinity decline lasting from 1966 to 1968 corresponded with a temperature increase. Then, as the salinity returned toward 35‰, the temperature also returned to the pre-1965 values. The first situation may mean that there were climatic shifts in the general northwest-southeast direction, parallel to the isotherms, thus causing a long-term change in the salinity but not in the temperature. In the second situation the climatic shift was first northward and then southward, affecting both temperature and salinity.

White (1975) described secular changes in baroclinic transport and morphology of the North Pacific subtropical gyre and indicated that during the years of low maximum transport the southwest portion of the gyre extended farther south than during the years of large transport. Similarly, it is possible that higher baroclinic flow and tightening of the gyre near Hawaii will result in lower salinity and a relaxation of flow will result in higher salinity. The long-term changes in the Koko Head salinity do not correspond with the changes described by White and are only in partial agreement with the supposition when tested against Wyrtki's (1974) North Equatorial Current index. The supposition, therefore, is in error or, the local wind induced surface flow, superimposed on the baroclinic flow, plays an important part in the long-term salinity changes.

At Christmas Island, in addition to the heat exchange and advection, the effect of wind-induced equatorial divergence is a process affecting the sea-surface temperature. Unfortunately, meteorological observations suitable for the calculation of heat exchange across the sea surface were not made on the island. Estimates made by Wyrtki (1966) and Seckel (1970) indicate the net heat exchange across the sea surface near Christmas Island to lie in the range of about 100 to 300 cal cm ^{2} day ^{1}. Assuming that the heat is distributed through a column of water 50 m deep, this process can produce temperature changes from about 0.6° to 1.8°C/mo. Temperature increases within this range are observed (Figure 3A).

An important term in the net heat exchange is the radiation from sun and sky that is affected in the equatorial region of the central Pacific by large variations in cloudiness (Bjerknes et al. 1969). The effect of such variability is most pronounced in late fall and early winter (Seckel 1970, figure 6). For example, the average net heat exchange near Christmas Island for November 1963 to January 1964 was calculated to be 177 cal cm ^{2} day ^{1}, and for the same months 1 yr later, 274 cal cm ^{2} day $^{-1}$. The average calculated radiation from sun and sky during the same periods was 372 cal cm ^{2} day ^{1} and 440 cal cm ^{2} day ^{1}, respectively, and accounted for 70% of the interyear difference in the net heat exchange. The Christmas Island water temperature declined in the first and rose in the second of these years (Figure 3A).

Heat gain across the sea surface cannot produce a temperature decline and, therefore, other processes must affect the temperature. One of these processes is heat advection that, at the Equator, is the product of the zonal current and the zonal temperature gradient. A raft designed for underwater biological observations was set out in February 1964 near the Equator at about long. 150°W and drifted westward 1,084 km (585 n.mi.) in 194 h (Gooding and Magnuson 1967) giving an average speed of 155 cm s^{-1}. A current with the speed of the raft, given a zonal temperature gradient of 0.5°C/10° of longitude, would produce a temperature change of more than 1.8°C/mo. A slower surface current, 30 cm s^{-1}, was observed on the Equator at long. 140°W during April 1958 (Knauss 1960). This current with the same zonal temperature gradient as before would produce a temperature decline of about 0.4°C/mo.

The South Equatorial Current indices presented by Wyrtki (1974) reflect large variability in the zonal current such as cited above. Additionally, monthly charts of sea-surface temperature (Eber et al. 1968) show the zonal gradient at the Equator to range from zero to >1°C/10° of longitude. Advection, therefore, is expected to play a large role in the temperature variations observed at Christmas Island.

Near the Equator the wind field is a key element in the evaporative heat loss, the cloudiness (affecting the radiation flux across the sea surface), upwelling, and in driving the equatorial currents. Quinn's (1974) southern oscillation (SO) index is related to the central South Pacific trade winds. It is not surprising, therefore, to find coherence in the changes of the SO index, Wyrtki's current index, and the Christmas Island temperature. Selecting the pronounced features of Figure 3B, declining SO index values during 1956, 1963, 1965, 1968, and 1971-72 correspond with rising temperatures. Increasing index values during 1964, 1966, and 1970 correspond with declining temperatures. During the first series of years South Equatorial Current speeds are declining and during the second series they are increasing.

SUMMARY

In this paper we have used harmonic analysis to make Koko Head temperature and salinity time series and Christmas Island temperature time series available for descriptive as well as numerical applications.

Time series data can be treated by a number of mathematical procedures in order to elicit important information. Initially, however, the presentation of the data in graphical form is most useful. The graphs in the appendices indicate the nature of the annual variations, and Figures 1, 2, and 3 indicate the nature of the long-term variations.

Although spectral analysis is not the objective of our work, the curve-fitting procedure further serves the descriptive purposes in that it permits separation of the time series into different scales of variability (panels B, C, D of Figures 1, 2, 3). For example, at Christmas Island the interannual temperature variation is as much as four times the average annual variation (Figures 3B, 5C). Equivalent figures of Koko Head salinity show that the interannual change can be about three times as large as the average annual variation.

Results of our analyses are also useful in numerical applications. Coefficients and phase angles (Appendices A, C, F) rather than observed values can be used for further calculations. In this manner the sampling variability apparent in the graphs of Appendices B and D is filtered out and variations of undesired duration can be omitted.

The separation of the time series into different scales of variability is a mathematical procedure and physical inferences must be made with caution. For example, Figures 2C and 3C show an annual cycle during every year although no annual cycle was apparent during 1957 in Figure 2A or during 1963, 1964, and 1965 in Figure 3A. The procedure does not indicate whether during these years the processes producing the annual cycle were absent or whether they were present but obscured by other processes. In another example, a 12-mo and a 6-mo sinusoid combine to reproduce the mean annual temperature cycle at Christmas Island. Again, the procedure does not indicate whether there exists a process affecting the temperature with a 6-mo periodicity.

Available information indicates that advection is an important process affecting the observed temperature and salinity variations. At Christmas Island large changes in the zonal component of the South Equatorial Current appear to cause large variations in advection. At Koko Head changes in the North Equatorial Current (Wyrtki

1974) do not correlate with the salinity changes, and variations in the meridional component of flow appear to cause the seasonal and long-term salinity changes.

On the basis of the long-term temperature curve at Koko Head (Figure 1B) one might conclude that interannual changes in environmental processes are unimportant. The Koko Head salinity curve (Figure 2B) shows such an inference to be incorrect and illustrates the value of monitoring more than one property at a location.

An understanding of the processes governing the temperature and salinity changes is pertinent to fishery management problems. Our speculations about these processes illustrate that good correlations between environmental properties and biological concentrations do not necessarily imply causal relationships. An example is the good correlation between skipjack tuna captures in the eastern Pacific yellowfin tuna regulatory area and central equatorial Pacific temperatures or the southern oscillation index, the skipjack tuna catches lagging about 18 mo.[5] Do these correlations mean that temperatures in the central equatorial Pacific determine larval survival and year-class strength or do they mean that the currents affect the concentration and distribution of skipjack tuna in the eastern Pacific with the temperature variations being ancillary? These questions are important if environmental factors are to be included in fishery population models.

ACKNOWLEDGMENTS

We thank A. Bakun, Pacific Environmental Group, NMFS, for helpful discussions; T. P. Barnett and W. C. Patzert, Scripps Institution of Oceanography, and J. Hayes, Fleet Numerical Weather Central, for reading the manuscript and making many useful comments; and M. J. Vitousek, Hawaii Institute of Geophysics, for making Christmas Island temperatures available to us.

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APPENDIX A

Sea-surface temperatures and salinities, Koko Head, Oahu, 1970-73: Phase angles and coefficients for harmonic functions.

$$S - K + bt + \sum_{n\ 1}^{k} C_n \cos \omega(nt - \alpha_n),$$

$$\omega = \frac{2\pi}{365}\ \text{days}^{-1},$$

t is the time in days beginning with the first day in each year.

APPENDIX A TABLE 1.—Phase angles and coefficients for sea-surface temperatures, Koko Head, 1970-73.

PHASE ANGLES IN DAYS

YEAR	N-VALUES 1	2	3	4	5	6	7	8	9	10	11	12	13
1970	72.20	-80.01	52.33	38.44	-1.41	50.88	-77.02	18.41	-89.79	85.22	-52.91	74.02	-84.68
1971	62.89	31.68	3.24	22.53	71.72	32.74	66.98	3.50	-10.93	-7.10	87.40	-80.98	-74.60
1972	62.93	21.24	66.54	-63.91	64.06	-70.46	83.06	-57.87	-46.34	-43.74	-8.51	76.71	24.69
1973	72.41	-4.17	-85.28	-59.54	-32.96	-89.25	-83.30	-50.69	57.26	-41.10	-19.01	-74.37	80.19

AMPLITUDES

YEAR	N-VALUES K	B	1	2	3	4	5	6	7	8	9	10	11	12	13
1970	25.5140	-0.0039	-1.8222	0.3590	-0.0552	-0.1421	-0.1264	-0.0868	0.1389	-0.1037	0.0876	-0.0646	0.0463	0.0780	0.0461
1971	24.7393	-0.0014	-1.3848	-0.3517	-0.1076	-0.1512	-0.1155	0.0318	-0.0722	0.0299	-0.1358	0.0295	0.0181	-0.0085	-0.0198
1972	24.4534	0.0003	-1.7160	-0.2903	0.0787	-0.1542	0.1731	-0.0360	-0.0577	0.0270	-0.0318	-0.0655	-0.0336	-0.0226	0.0417
1973	23.7849	0.0036	-1.0235	-0.0600	-0.1372	-0.1433	-0.1347	-0.0319	-0.0484	0.0860	0.0569	-0.0463	-0.0632	0.0468	0.0724

APPENDIX A TABLE 2.—Phase angles and coefficients for sea-surface salinities, Koko Head, 1970-73.

PHASE ANGLES IN DAYS

	N-VALUES												
YEAR	1	2	3	4	5	6	7	8	9	10	11	12	13
1970	75.16	-60.43	16.34	70.03	35.34	30.83	-37.70	-38.82	-26.93	-46.86	-77.26	21.73	-2.76
1971	-51.94	-80.21	-63.27	24.14	-45.10	-73.97	60.91	76.63	-34.16	-67.62	-14.74	36.53	-53.75
1972	9.27	-51.54	-89.46	-72.61	-11.74	-20.48	61.79	78.55	59.38	84.94	10.15	24.89	-24.50
1973	-82.26	88.25	23.40	-17.29	1.01	-27.39	-65.68	-60.90	37.04	90.17	-3.22	-50.96	2.98

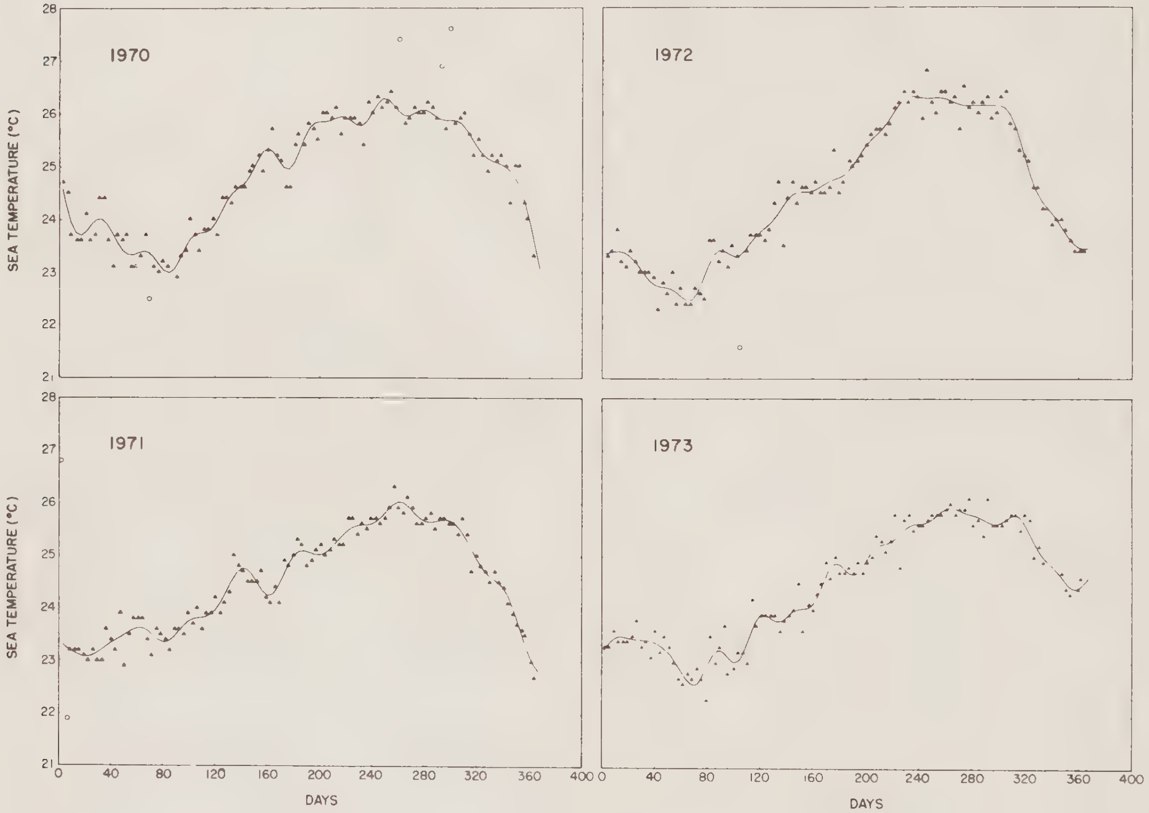
AMPLITUDES

	N-VALUES														
YEAR	K	B	1	2	3	4	5	6	7	8	9	10	11	12	13
1970	34.8321	0.0009	0.0691	-0.0482	-0.0141	0.0196	0.0353	0.0107	-0.0073	0.0024	0.0002	0.0033	0.0059	-0.0115	-0.0105
1971	35.0025	0.0002	0.1115	-0.0132	0.0050	0.0111	-0.0078	0.0208	0.0160	-0.0036	0.0126	-0.0134	-0.0084	-0.0027	-0.0096
1972	34.9629	0.0	0.1838	-0.0807	0.0324	0.0365	0.0209	-0.0133	-0.0010	-0.0046	0.0127	0.0157	-0.0052	0.0089	-0.0085
1973	35.0231	-0.0002	0.0960	0.0213	0.0250	0.0341	0.0401	-0.0057	-0.0190	-0.0220	-0.0207	-0.0270	-0.0018	-0.0116	-0.0175

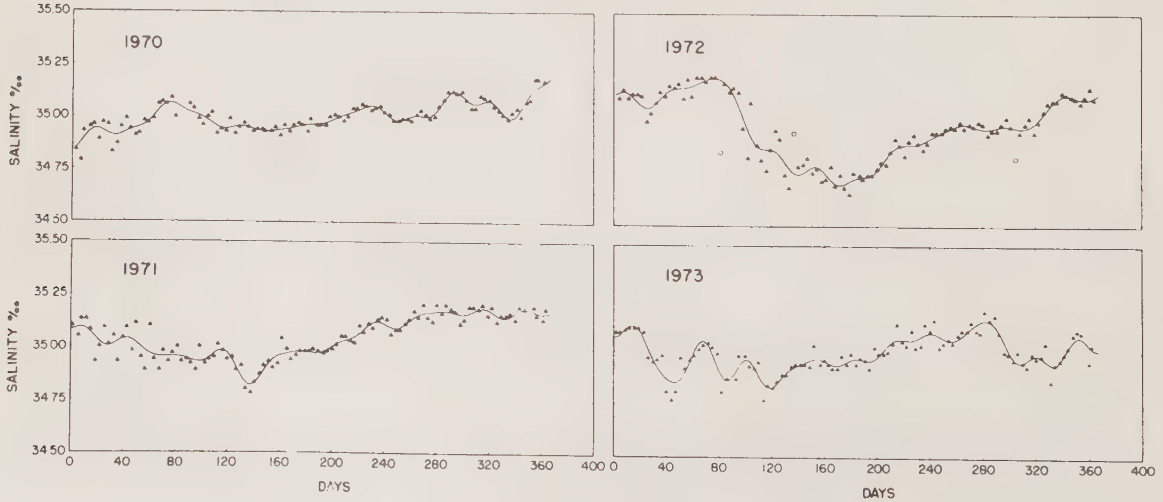
APPENDIX B

Sea-surface temperatures and salinities, Koko Head, Oahu, 1970-73: Fitted curves with observed values for each year.

Note: Circled observations have not been used in the harmonic analysis.



APPENDIX B FIGURE 1.—Sea-surface temperatures, Koko Head, 1970-73.



APPENDIX B FIGURE 2.—Sea-surface salinities, Koko Head, 1970-73.

APPENDIX C

Sea-surface temperatures, Christmas Island, 1970-73: Phase angles and coefficients for harmonic functions for each quarter of the year.

Days 1 to 120 = First quarter,
91 to 210 = Second quarter,
181 to 300 = Third quarter,
271 to 390 = Fourth quarter, extending 25 days into new year,

$$S = K + bt + \sum_{n=1}^{k} C_n \cos \omega (nt - \alpha_n),$$

$$\omega = \frac{2\pi}{120} \text{ days}^{-1},$$

t is the time in days beginning with the first day of each quarter.

PHASE ANGLES IN DAYS

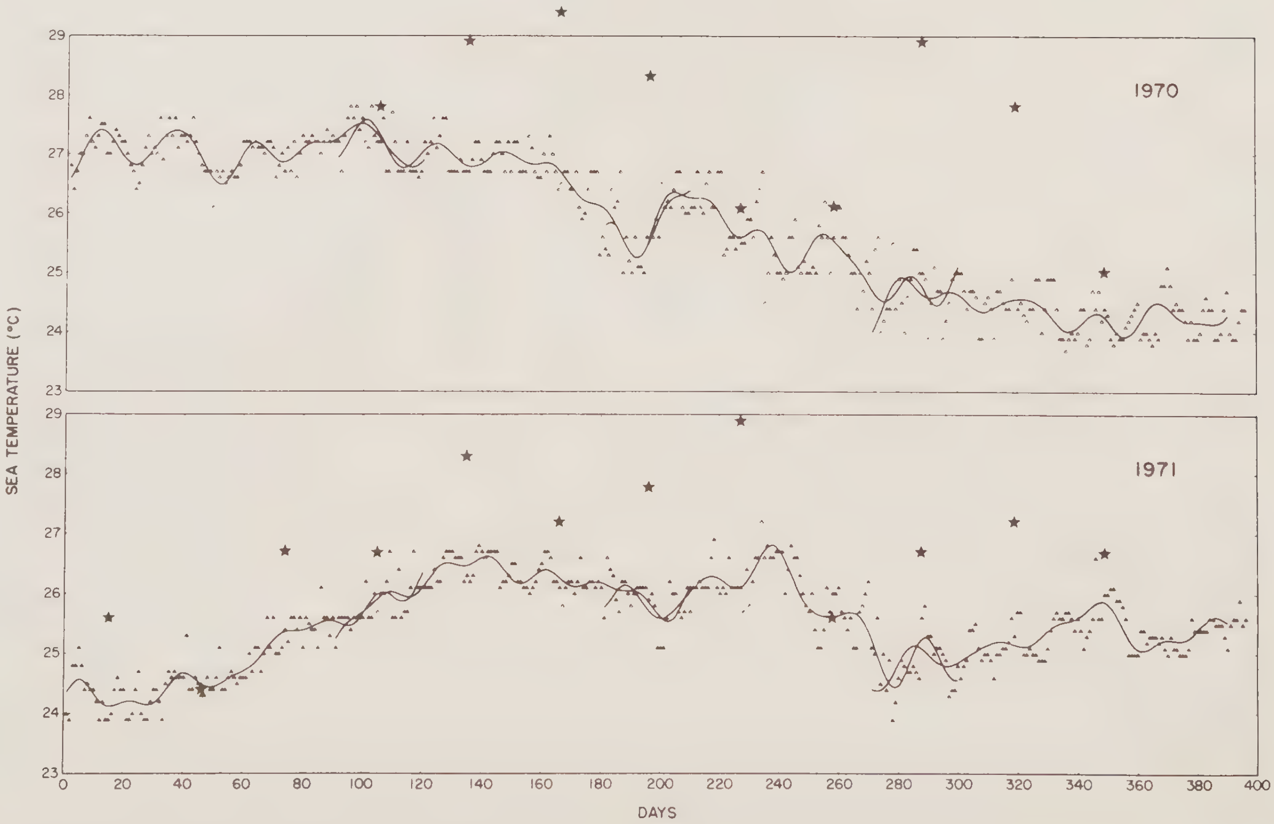
		N-VALUES						
YEAR	QU.	1	2	3	4	5	6	7
1970	1	12.44	-6.13	-16.78	-28.73	-2.08	6.81	16.58
	2	-22.81	17.61	7.60	14.33	0.98	13.95	-6.74
	3	-22.04	-10.25	-16.75	28.25	20.57	9.51	18.38
	4	26.63	-22.46	-18.15	-13.17	25.90	16.12	3.83
1971	1	-9.01	18.72	0.88	-23.22	-19.97	23.78	26.91
	2	-14.62	-11.07	-29.19	-19.30	18.78	-28.03	12.39
	3	-3.95	-4.74	8.40	-13.89	-2.60	-5.05	-20.05
	4	-7.34	24.95	-13.18	3.21	11.76	-16.66	25.18
1972	1	7.89	-27.53	-29.51	-14.94	-26.14	12.85	-22.64
	2	-7.77	-27.22	20.06	4.35	-1.33	21.18	19.69
	3	-6.13	-10.93	-15.60	29.25	28.39	21.23	18.53
	4	1.16	21.36	11.98	1.52	24.55	0.57	-19.27
1973	1	28.56	26.13	9.53	-4.76	-15.17	26.74	24.63
	2	28.96	21.19	12.08	25.17	-8.93	-29.78	-13.43
	3	23.99	-18.26	7.15	-11.40	-20.11	-13.68	16.48
	4	17.68	26.83	-28.88	27.12	-18.74	-21.21	18.01

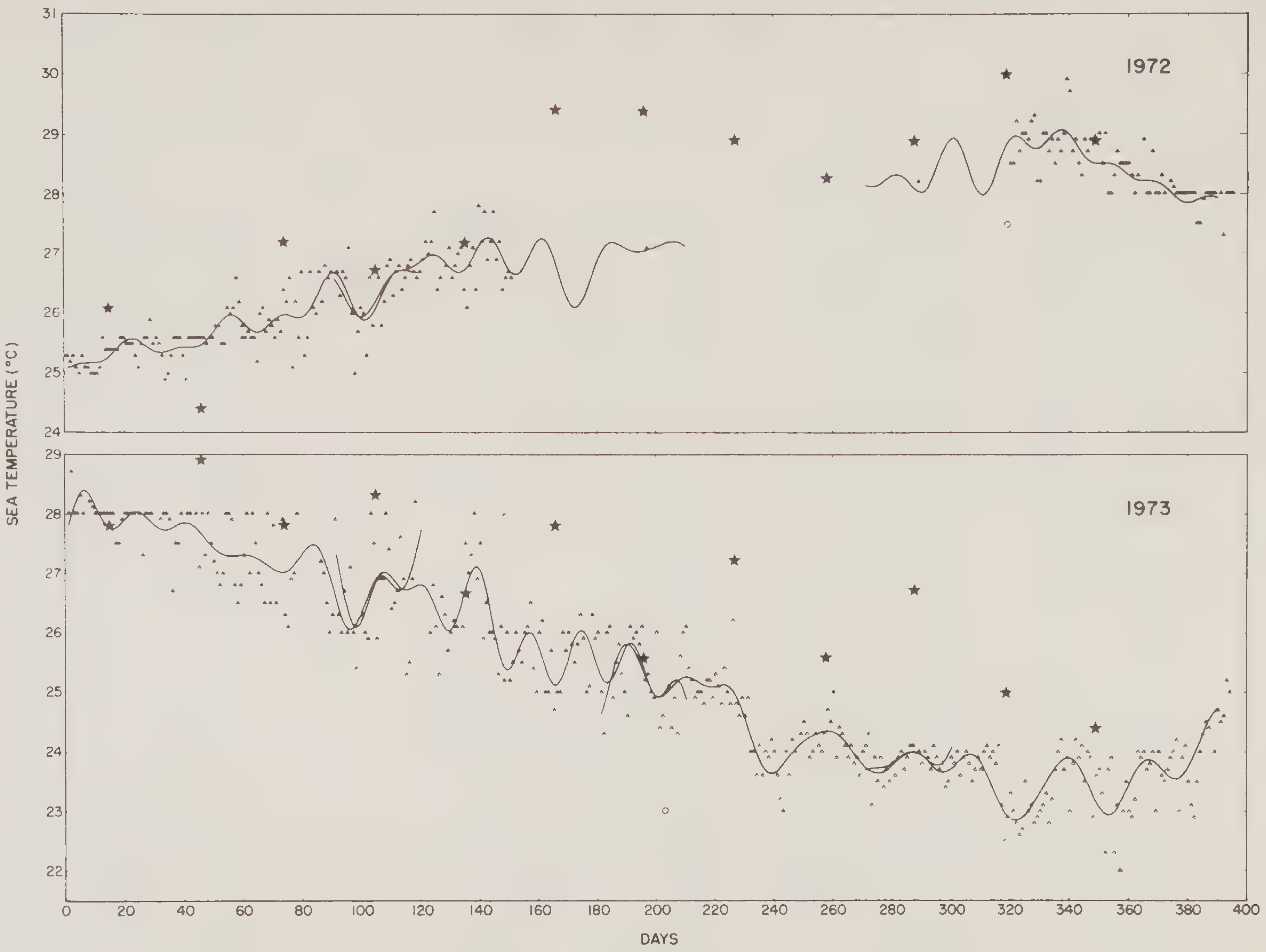
AMPLITUDES

				N-VALUES						
YEAR	QU.	K	B	1	2	3	4	5	6	7
1970	1	26.8641	0.0034	0.0851	-0.1983	-0.0753	-0.2552	-0.1641	0.0452	-0.0599
	2	26.8841	-0.0041	-0.4763	0.3681	0.1609	0.0824	-0.0936	-0.1511	-0.0466
	3	25.7091	-0.0049	-0.4564	-0.2126	0.1819	-0.0754	0.1993	0.0843	0.1654
	4	24.1813	0.0033	0.3638	-0.1038	-0.1890	-0.0981	0.1259	-0.0722	-0.0883
1971	1	23.9165	0.0176	0.1871	0.0905	0.1309	-0.1024	-0.0435	0.0735	0.1056
	2	25.6009	0.0083	-0.5389	-0.1219	-0.1488	-0.1029	0.0518	0.0146	0.0975
	3	26.3106	-0.0098	-0.5171	0.2021	0.0472	0.1281	-0.2729	-0.0850	-0.0912
	4	24.6692	0.0091	-0.2184	0.2117	0.0760	-0.1346	-0.0573	0.0830	-0.0717
1972	1	25.0308	0.0133	0.0496	-0.0682	-0.0819	0.1725	0.0891	-0.0918	-0.1120
	2	26.5641	0.0038	-0.1173	0.2415	-0.1913	0.0576	0.2075	-0.1676	0.1233
	3	27.3256	0.0120	-0.2914	-0.5543	0.5778	-0.2506	0.7280	-0.1929	-0.6557
	4	28.5013	-0.0019	-0.3996	0.1060	-0.0935	.1104	0.1171	-0.1484	0.1384
1973	1	27.2621	0.0017	0.6704	0.3264	0.2433	0.0114	-0.1570	0.2590	0.0926
	2	27.3407	-0.0223	-0.1509	-0.3212	-0.0538	-0.2381	0.1734	-0.0976	0.3913
	3	24.6561	-0.0033	0.6202	-0.2669	0.2438	-0.2662	-0.1172	-0.1539	-0.0632
	4	23.0800	0.0092	0.5485	0.2358	0.1139	0.2970	0.1569	0.1038	0.0243

APPENDIX D

Sea-surface temperatures, Christmas Island, 1970-73: Fitted curves with observed values for each year. Circled observations have not been used in the harmonic analysis. Stars indicate values taken from *Fishing Information*.





APPENDIX D FIGURE 1.— Sea-surface temperatures, Christmas Island, 1970-73: Fitted curve with observed values for each year. Circled observations have not been used in the harmonic analysis. Stars indicate values taken from *Fishing Information* (see text footnote 3).

APPENDIX E

APPENDIX E TABLE 1.—Standard error of estimate (°C) for each annual temperature function at Koko Head, 1970-73, with harmonic analysis carried out in sequence to $n = 1, 2, 3, \ldots$ and 13.

Year	*n*-values 1	2	3	4	5	6	7	8	9	10	11	12	13
1970	0.41	0.32	0.32	0.30	0.29	0.28	0.26	0.25	0.24	0.24	0.23	0.22	0.22
1971	0.37	0.26	0.25	0.23	0.22	0.22	0.21	0.21	0.18	0.18	0.18	0.18	0.18
1972	0.35	0.29	0.28	0.26	0.23	0.23	0.22	0.22	0.22	0.22	0.21	0.21	0.21
1973	0.29	0.29	0.28	0.26	0.24	0.24	0.23	0.23	0.22	0.22	0.22	0.21	0.21

APPENDIX E TABLE 2.—Standard error of estimate (‰) for each annual salinity function at Koko Head, 1970-73, with harmonic analysis carried out in sequence to $n = 1, 2, 3, \ldots$ and 13.

Year	*n*-values 1	2	3	4	5	6	7	8	9	10	11	12	13
1970	0.055	0.043	0.042	0.040	0.031	0.030	0.029	0.029	0.029	0.029	0.029	0.027	0.026
1971	0.047	0.046	0.046	0.045	0.044	0.042	0.040	0.040	0.039	0.038	0.037	0.037	0.036
1972	0.080	0.058	0.054	0.047	0.044	0.043	0.043	0.043	0.042	0.041	0.040	0.040	0.040
1973	0.068	0.066	0.064	0.059	0.052	0.051	0.050	0.047	0.045	0.040	0.040	0.039	0.037

APPENDIX E TABLE 3.—Standard error of estimate (°C) for each quarterly temperature function at Christmas Island, 1970-73, with harmonic analysis carried out in sequence to $n = 1, 2, 3, \ldots$ and 7.

Year	Quarter	*n*-values 1	2	3	4	5	6	7
1970	1	0.35	0.32	0.31	0.25	0.23	0.22	0.22
	2	0.46	0.37	0.35	0.35	0.34	0.32	0.32
	3	0.50	0.47	0.46	0.45	0.43	0.43	0.42
	4	0.39	0.38	0.36	0.35	0.34	0.33	0.33
1971	1	0.30	0.30	0.28	0.27	0.27	0.27	0.26
	2	0.30	0.29	0.27	0.26	0.25	0.25	0.24
	3	0.42	0.39	0.38	0.37	0.33	0.32	0.32
	4	0.34	0.31	0.30	0.29	0.28	0.28	0.27
1972	1	0.36	0.35	0.35	0.33	0.32	0.32	0 31
	2	Data sets incomplete or missing						
	3							
	4							
1973	1	0.64	0.60	0.59	0.59	0.58	0.55	0.55
	2	0.71	0.68	0.69	0.66	0 65	0.64	0.58
	3	0.53	0.49	0.46	0.42	0.41	0.40	0 39
	4	0.46	0.43	0.43	0.37	0.35	0.34	0.34

APPENDIX F

Harmonic coefficients for the long-term series. Coefficients for each harmonic term in the series

$$S = a + bt + A_0 + \sum_n (A_n \cos n\omega t + B_n \sin n\omega t)$$

are given in the tables below. Harmonic analysis was performed on the residuals from a linear fit. If t is in months, for the Koko Head series, $\omega = \frac{2\pi}{216}$, and the first month in January 1956; for the Christmas Island series, $\omega = \frac{2\pi}{240}$, and the first month is January 1954.

APPENDIX F TABLE 1.—Coefficients for Koko Head temperature. $a = 23.7009$, $b = 0.0020$.

	0	1	2	3	4	5	6	7	8	9
					A_n					
0	0.5478	−0.1755	−0.1397	0.1131	0.0279	−0.0538	0.0263	0.0583	−0.0782	−0.0245
10	0.0174	0.0760	−0.0642	0.0401	0.0905	0.0168	−0.0439	0.0641	−0.2483	−0.0055
20	0.1262	−0.0126	−0.0035	−0.0263	0.0408	−0.0211	−0.0253	−0.0235	0.0576	−0.0279
30	−0.0428	0.0019	−0.0060	0.0497	−0.0114	0.0191	−0.0134	−0.0348	−0.0041	−0.0258
40	0.0332	0.0042	−0.0024	−0.0502	0.0274	0.0056	0.0239	−0.0040	−0.0171	−0.0274
50	0.0377	−0.0436	0.0015	−0.0116	−0.1030	0.0298	0.0257	0.0154	−0.0007	0.0068
60	0.0162	−0.0113	−0.0050	−0.0267	0.0202	0.0202	0.0231	−0.0107	0.0145	−0.0234
70	−0.0174	0.0117	−0.0067							
					B_n					
0	—	0.0887	0.2135	0.1425	0.0305	0.0989	0.0023	0.0552	0.0418	0.0052
10	0.1329	0.0093	0.0696	0.0044	0.0437	−0.0274	0.0195	−0.0056	−1.4540	0.0197
20	0.0262	0.0509	0.0531	0.0198	0.0676	0.0572	−0.0049	0.0035	0.0105	−0.0409
30	−0.0313	0.0422	−0.0177	−0.0767	−0.0058	0.0373	−0.1468	−0.0175	0.0347	0.0226
40	0.0519	0.0306	0.0078	−0.0188	−0.0288	0.0258	0.0207	−0.0533	0.0105	−0.0327
50	0.0151	−0.0145	0.0652	−0.0230	−0.0113	−0.0283	−0.0074	0.0238	0.0050	0.0090
60	0.0188	−0.0138	0.0200	0.0272	−0.0316	−0.0222	0.0053	−0.0254	0.0177	−0.0083
70	0.0011	−0.0167	−0.0020							

APPENDIX F TABLE 2.—Coefficients for Koko Head salinity. $a = 35.0141$, $b = 0.0001$.

	0	1	2	3	4	5	6	7	8	9
					A_n					
0	−0.1228	0.0366	0.0685	−0.0653	−0.0894	0.0441	−0.0034	−0.0048	0.0165	0.0163
10	0.0286	−0.0017	0.0109	−0.0128	−0.0156	0.0024	0.0043	0.0093	0.0903	−0.0020
20	−0.0004	−0.0095	0.0032	−0.0127	0.0017	−0.0035	0.0020	−0.0101	−0.0034	0.0028
30	0.0020	0.0117	−0.0043	−0.0097	−0.0132	−0.0023	−0.0091	0.0094	−0.0067	−0.0039
40	−0.0057	0.0085	0.0070	0.0040	−0.0136	−0.0098	−0.0035	0.0041	0.0030	−0.0053
50	−0.0031	−0.0062	0.0070	0.0130	−0.0002	−0.0092	−0.0053	−0.0002	0.0064	0.0046
60	−0.0006	−0.0048	−0.0039	−0.0021	0.0013	−0.0008	−0.0063	0.0002	0.0014	−0.0022
70	0.0089	−0.0016	0.0028							
					B_n					
0	—	0.0663	−0.0287	−0.0063	0.0206	0.0174	−0.0532	0.0026	−0.0221	0.0006
10	−0.0372	−0.0034	−0.0095	−0.0047	0.0268	−0.0041	0.0007	−0.0199	0.0085	0.0034
20	−0.0099	−0.0050	−0.0075	−0.0012	−0.0108	0.0020	0.0058	0.0075	0.0131	0.0026
30	0.0109	0.0028	0.0088	0.0086	−0.0105	−0.0095	0.0021	0.0126	0.0043	0.0138
40	−0.0050	−0.0067	−0.0039	0.0158	−0.0005	−0.0121	−0.0124	0.0064	0.0125	0.0092
50	−0.0002	0.0028	0.0037	0.0001	0.0050	0.0003	0.0001	−0.0089	−0.0003	−0.0000
60	0.0074	0.0108	−0.0071	−0.0070	0.0059	−0.0028	0.0028	0.0049	−0.0011	0.0007
70	0.0072	−0.0021	0.0015							

APPENDIX F TABLE 3.—Coefficients for Christmas Island temperature. $a = 26.1443$, $b = -0.0054$.

	0	1	2	3	4	5	6	7	8	9
					A_n					
0	1.5694	−0.2024	−0.3409	−0.1310	0.1924	0.3505	−0.1455	−0.4605	−0.1400	−0.2839
10	0.1658	−0.3162	0.0228	−0.2507	−0.0381	0.1309	0.2614	0.0088	−0.0257	0.0569
20	−0.4204	−0.0517	0.0635	0.0676	0.0431	0.0179	0.0014	−0.0727	−0.0298	−0.0637
30	0.0295	−0.0316	−0.0583	−0.0133	0.0264	0.0040	0.0073	−0.0021	−0.0587	−0.0397
40	0.1025	−0.0243	−0.0049	0.0496	−0.0108	0.0176	0.0054	−0.0458	0.0351	−0.0144
50	0.0100	0.0321	0.0211	−0.0272	0.0145	−0.0076	0.0085	0.0031	−0.0410	0.0141
60	0.0369	−0.0001	0.0292	−0.0495	−0.0385	−0.0080	−0.0065	0.0232	−0.0204	0.0170
70	0.0134	0.0126	−0.0021	−0.0141	0.0203	−0.0178	−0.0085	0.0325	0.0144	0.0445
80	0.0022									
					B_n					
0	—	−0.8028	−0.2146	−0.6457	−0.4963	−0.3942	−0.3880	0.1339	−0.1839	0.0969
10	−0.1253	0.1038	0.1556	−0.0039	0.0555	0.2400	0.1030	0.1198	−0.0589	0.1246
20	0.0883	0.0041	0.0403	−0.1501	−0.0233	0.0791	−0.0622	−0.0063	0.0252	0.0138
30	0.0456	0.0172	0.0133	−0.0420	−0.0357	0.0625	0.0097	0.0054	0.0347	−0.0026
40	−0.1791	−0.0090	0.0979	−0.0668	−0.0407	0.0247	0.0003	−0.0241	0.0154	−0.0151
50	0.0073	0.0230	0.0144	0.0196	−0.0277	−0.0250	0.0374	−0.0110	0.0054	0.0258
60	−0.0250	0.0336	−0.0219	−0.0223	−0.0124	−0.0314	0.0035	−0.0044	0.0041	0.0267
70	−0.0323	0.0071	−0.0183	−0.0084	0.0289	−0.0417	0.0431	−0.0055	0.0038	0.0022
80	0.0022									

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NOTES

ENERGY FOR MIGRATION IN ALBACORE, *THUNNUS ALALUNGA*

The relations between immigrants and residents of a specific fishing ground can likely be evaluated from examination of the relative fat content of individuals from a time sequenced sampling of the fishery. These kinds of information are not yet estimable for pelagic populations.

The problem of energy availability and utilization in migrations of fish is a perplexing one. Migrations are energetically quite expensive unless a fish is passively carried by currents. Recently recorded migrations of two tagged albacore, *Thunnus alalunga* (Bonnaterre), across the Pacific Ocean indicate that they traveled an average of 48 km/day (Japanese Fisheries Agency 1975). As these fish were approximately 80 cm long on release, the average migration speed was about 0.65 body lengths/s (55.6 cm/s). This is well within the range of observed swimming speeds for this species. These albacore were reported to have traveled from lat. 35°44′N, long. 171°37′E (Figure 1, point E) to lat. 47°00′N, long. 125°30′W (Figure 1, point F), a distance of 5,239 km in 110 days. The caloric equivalent, in grams of fat,[1] utilized by these two fish at the estimated rate of travel of about 55 cm/s would be about 1,450 g or 14.5% of their expected weight at the onset of migration. Although great amounts of feed would not be necessary for this migration given the 1 kcal/g average available caloric content for forage (Sharp and Francis 1976), the albacore has been reported to have up to 18.2% fat in the edible flesh portions (Sidwell et al. 1974). Muscle tissue constitutes 58.2% of the total body weight of albacore (Dotson unpubl. data) which means up to 10.6% body weight in fat has been observed, a value approaching that necessary to provide the caloric energy for these migrations.

There is little doubt that albacore do not migrate directly, that feeding does occur, and that the fish probably do grow in overall length and

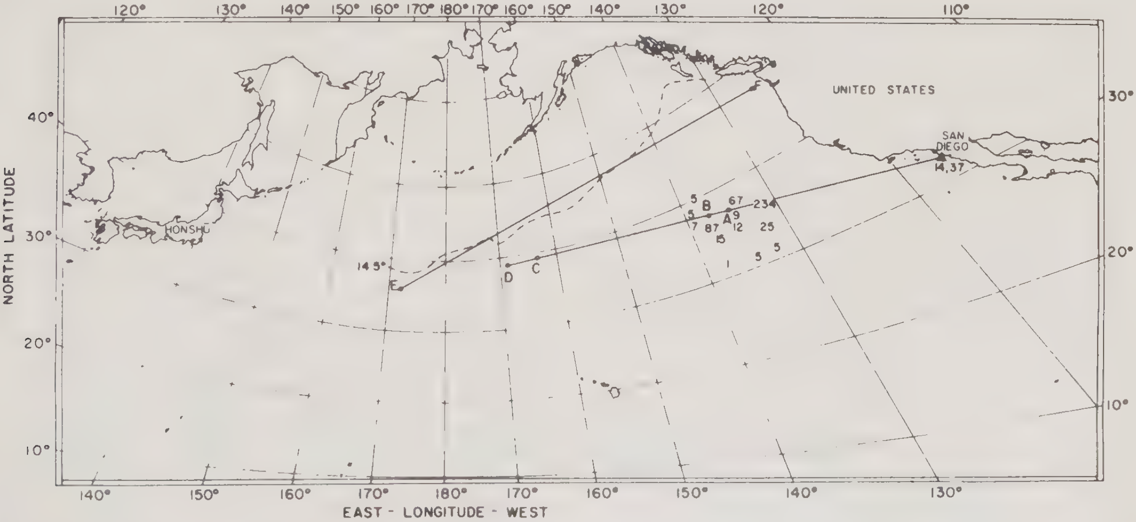

FIGURE 1.—A great circle plotting chart is shown and the quantity and location of albacore samples is indicated by the numerals. A length-mass equation was developed for the 477 albacore caught west of long. 130°W during June 1974. The numbers 14 and 37 near San Diego represent the samples collected in July and September 1975, respectively. Using ▲ as the origin the letters A and B along the line represent the distances which a 63-cm albacore could swim utilizing 404 g of fat at A, its minimum speed; B, the observed diurnal-nocturnal activity level. Points C and D on the same line represent the distance that the 65-cm fish with the greatest observed mass deficit (999 g) could have traveled utilizing the energy of this quantity of fat at the two respective activity levels described above. Points E and F are the release and recapture positions of two albacore tagged by Japanese researchers. The minimum temperature habitat limit of albacore (14.5°C) is depicted by a dashed line. The great circle route does not differ markedly from this boundary but likely represents a conservative estimate of the total distance traveled between points E and F.

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[1] 9.4 kcal/g fat.

mass during the migratory period. What appears to be an important question is whether or not the migrations of albacore and other tunas are extra demanding, meaning sufficient short-term energy is required to induce fat store utilization even though feeding is still accomplished. Too often the concepts of growth and fat deposition are integrated such that it is considered unlikely that morphological growth can take place during fat store utilization. Certainly from observations of adolescent growth in mammals it is obvious that there is no necessary dichotomy here. The two processes require separate biochemical pathways and are very likely separated temporally, well within the standard day.

In a preliminary effort to examine the question of fat utilization, the length-mass relationship of albacore collected offshore preceding their appearance in the onshore eastern Pacific surface fishery has been compared with fish freshly arrived in this fishery, and with fish which have presumably been grazing and reconditioning for the postsummer exodus from the onshore area. Calculations from these data support the hypothesis that fat stores are utilized for migration energy.

We hope that these calculations and subsequent inferences will stimulate further research into the considerable problem of highly variable length-mass information and its potential use in studies of migratory fishes.

Observations

In June 1974, 477 albacore 463 to 794 mm long were captured in the area between long. 130° to 140°W and lat. 30° to 40°N (Figure 1). A curve was fitted by regression to the length-mass data from these fish resulting in the equation (Dotson 1977),

$$M = 4.514 \times 10^{-5} L^{2.8746} \qquad (1)$$

where M is the mass in grams and L the fork length in millimeters. Measured values fell within 250 g of the regression line.

Mass and length measurements were made on 14 albacore (600 to 657 mm FL, mean 631) collected during July and 37 fish (516 to 851 mm FL) collected during September 1975, in a region 110 km south of San Diego, Calif. (Figure 1). The mass of September-caught albacore was not different from those estimated by the length-mass regression curve. The mass of July-caught albacore, however, averaged 404 g below those estimated by regression (range: 172 g greater to 999 g less). Analysis of body densities indicated that the mass deficit of the albacore caught in July was probably due to fat loss, or simply stated, as a fish of a given length gets lighter its density increases (Dotson 1977).

The albacore fishery near the coast commenced in July 1975. The albacore in this fishery are known to migrate from the offshore region (Laurs and Lynn in press), and it is assumed, therefore, that the mass (fat) deficit was utilized as an energy source during migration to the coast.

Calculations and Inferences

Using the observed mass deficits observed in the July 1975 sample, it is possible to estimate the migration path length assuming 1) little or no growth occurs during the migration, and 2) the fat utilized is the only energy source during migration.

Based upon studies of swimming energetics of tunas, Sharp and Francis (1976) estimated the relation between swimming speed (V) in centimeters per second, fork length (l) in centimeters, and the swimming caloric expenditure per unit time (C_s) in kilocalories per hour. The basic equation for this relation, in calories utilized per hour, is as follows:

$$C_s = 8.7 \times 10^{-8} (l)^2 (V)^3 \, Cd. \qquad (2)$$

The coefficient of drag (Cd) is estimated using the relation (Sharp and Francis 1976)

$$Cd = 0.262 \exp\left[-(4.805 \times 10^{-6}) Re\right] \qquad (3)$$

where Re (Reynolds number) = lV/ν (at $Re \geqslant 6.8 \times 10^5$, $Cd = 0.01$), ν is the kinematic viscosity of seawater, approximated by the value 0.01.

Sharp and Francis (1976) also estimated the metabolic maintenance energy (C_m) (i.e. stasis energy requirements) for tunas to be 1 g cal/g per h. The metabolic weight (W_{met}) is approximated by the relation

$$W_{\text{met}} = (M_f)^{0.8} \qquad (4)$$

$$C_m = W_{\text{met}} \times 10^{-3} \text{ kcal/g per h} \qquad (5)$$

where M_f is the mass of the fish in grams.

Assuming that the mean mass deficit of 404 g of the albacore caught in July was fat loss and given that fat yields about 9.4 kcal/g, less ~15% due to the cost of fat mobilization (SDA), leaving about 8.0 kcal/g, the caloric value of the fat loss is 3,272 kcal. The mean length of the albacore in the July sample was 63 cm with a computed mass for the offshore region (from Equation (1)) of 5,030 g. As this would be the weight at the initial stage, it seems appropriate to use as the mass for the calculations the equivalent of one-half of the observed loss in mass (202 g) subtracted from the computed initial mass to give a value of 4,828 g. Using these equations, the rate of caloric expenditure per hour was estimated for a 63-cm albacore swimming at 54 cm/s which is the estimated minimum speed a 63-cm albacore can swim and maintain hydrostatic equilibrium, V_{100} (Magnuson 1970; Dotson 1977). Where C_s plus C_m is equal to the total caloric expenditure (C_{total}) during migration, then:

$$\begin{aligned} C_{\text{total}} &= C_s + C_m \\ &= 2.78 \text{ kcal/h} + 0.89 \text{ kcal/h} \\ &= 3.67 \text{ kcal/h}. \end{aligned} \tag{6}$$

The caloric equivalent of the fat divided by the hourly caloric utilization rate, C_{total}, Equation (6) yields the number of hours that swimming at 54 cm/s could be sustained utilizing this energy source alone and is estimated to be

$$\frac{3{,}272 \text{ kcal}}{3.67 \text{ kcal/h}} = 892 \text{ h or } {\sim}37 \text{ days.}$$

The speed and time multiplied together yield the linear distance traveled during this period. This was calculated to be 1,730 km (935 nmi).

Based upon sonic tracking experiments, the average swimming speeds of three albacore 84, 85, and 87 cm in length have been observed to be 95 cm/s during the day and 62 cm/s at night (Laurs et al. 1977). The minimum swimming speed for hydrostatic equilibrium of these fish (V_{100}) is estimated to be about 42 cm/s (Dotson 1977). Assuming the ratio of observed speed (V_0) to minimum speed (V_{100}) to be relatively constant over the size range, then diurnal and nocturnal speeds can be estimated where V_0/V_{100} = 42 cm/s = 2.260 is the multiplier for daylight speeds and (62 cm/s)/(42 cm/s) = 1.575 is the multiplier for night speeds. The result of this estimation is that the daylight and nighttime speeds for a 63-cm albacore are 122 and 80 cm/s, respectively. Assuming equal time spent at each speed, about 6.08 kcal/h are utilized. If the tracking observations are representative of migratory swimming speed, and therefore caloric expenditures, then the fat energy would have been utilized in a period of nearly 22 days and the linear distance traveled would be about 1,960 km (1,060 nmi).

From the nearshore area of capture, the maximum linear distance traveled using the average fat loss of a 63-cm albacore is indicated by points A and B in Figure 1. The two values indicated represent a) 37 days at a minimum speed of 54 cm/s, and b) the estimated diurnal rates of 80 and 122 cm/s for equal portions of 22 days. The interesting result is that both the distances are within the area where the offshore samples with the greater length-mass relationship were collected and compared with the onshore material.

The maximum observed mass difference from the offshore mean of an albacore caught inshore is 999 g or 18% of its body weight for a 65-cm fish (Dotson 1977). Assuming the total weight difference to be fat, at its calculated minimum speed of 54 cm/s, this albacore could have traveled 4,200 km (2,270 nmi) over a period of 90 days utilizing only this fat as an energy source. This would place the fish well out in the mid-Pacific, as shown by point C in Figure 1. Swimming at the estimated day and night speeds of 122 and 80 cm/s for equal parts of the day this fish could travel 4,680 km (2,520 nmi) in 54 days (Figure 1, point D).

These observations, calculations, and hypotheses should indicate some of the potential effects which can be examined in the future, given broadscale sampling and interest in the migrations of tunas. Fat content is an important indicator of the calories available for migration and/or spawning in fish of sufficient maturity. The importance of immigrants to population assessment in managed fisheries is obvious. Certainly, spawning success and behavior is dependent upon the available caloric stores. For tunas where migration and grazing up to spawning condition may be competitive processes, a thorough examination of the fat level cycles may offer insights into both periodicity and location of the potential spawners. This is an area of minimal understanding in tunas to date. Considering the importance of these processes in the life cycles of tunas, it seems that a certain amount of importance should be placed upon obtaining comprehensive data from several behavioral categories of tunas where inferences could be made about the relation of fat stores and behavior.

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A Summary of the Tuna Baitfish Workshop

RICHARD S. SHOMURA[1]

An invitational workshop on tuna baitfish problems, cosponsored by the National Marine Fisheries Service and the University of Hawaii Sea Grant College, was held at the Honolulu Laboratory, Southwest Fisheries Center, on 4-6 June 1974. The central issues addressed by the workshop dealt with the problem of securing adequate supplies of bait to support the development or expansion of skipjack tuna, *Katsuwonus pelamis*, fishing in the central and western tropical Pacific.

The 38 participants (see Appendix A for list of participants) from the mainland United States, Hawaii, Japan, and islands of the western Pacific reviewed and discussed a number of background papers prepared for the workshop. These background documents make up the bulk of the papers provided in this volume.

The workshop was organized around three sessions which focused attention on 1) natural stocks of baitfish, 2) culture of suitable baitfish species, and 3) transporting and holding bait and substitute baits. These sessions were preceded by a general review of baitfish problems and a discussion on the criteria for a good baitfish species. The workshop concluded with a general summary session. The following brief review of the workshop should provide the reader with a framework for relating the individual papers of this volume.

TUNA FISHING AND THE BAITFISH PROBLEM

Presently the only two economically viable methods of catching tuna in commercial quantities in tropical waters are purse seining and pole-and-line fishing with live bait. The expansion of tuna fishing in the central and western tropical Pacific is currently limited by certain technical problems associated with both methods of fishing. Purse seine trials conducted thus far in the central and western tropical Pacific using conventional seines have resulted in a success rate much lower than that enjoyed in the eastern tropical Pacific tuna fishery. It is generally believed that the clear waters and deep thermoclines of the central and western Pacific make it possible for tuna, especially skipjack tuna, to avoid capture by conventional purse seines. Thus, new net designs or new fishing techniques will have to be developed before purse seining can become a widespread, economically successful method of fishing in these waters.

The major problem associated with development or expansion of existing pole-and-line tuna fisheries in the central and western tropical Pacific is the lack of adequate supplies of baitfish. In the most severe cases suitable baitfish species are lacking altogether. In many areas of the Pacific, e.g. American Samoa, the stocks of naturally occurring baitfish species are inadequate to support even a small domestic tuna fishery. In other areas, baitfish may occur only in small quantities, limiting catches of tuna to a point far below the probable level of optimum sustainable yield.

In Hawaii and the Western Carolines, the supply of baitfish has been sufficient for the operation of only small fleets of tuna vessels. The Hawaiian fishery is conducted by 12 to 15 boats, generally less than 90 ft in length, which annually land about 4,500 t of skipjack tuna. Based on skipjack tuna surveys and an analysis of the fishery conducted several years ago by the National Marine Fisheries Service, it is believed that the catch of the Hawaiian fishery could be increased in direct proportion to an increase in fishing effort. However, because successful purse seine fishing in these waters seems technologically unfeasible at this time, the increase in tuna fishing effort can only be achieved by an increase in pole-and-line fishing effort. While the problems faced by the Hawaiian tuna fishery are complex, a basic constraint has been the limited supply of suitable baitfish. A similar situation exists in the Western Carolines.

In developing their southern fishery for skipjack tuna, the Japanese have overcome the lack of locally available baitfish by transporting baitfish from the Japanese home ports. Despite the problems of transporting an anchovy species, *Engraulis japonicus*, which is native to colder waters of the higher latitudes into tropical waters, the Japanese southern fishery has expanded to a present annual catch exceeding 100,000 t/yr.

CRITERIA OF GOOD BAITFISH SPECIES

The workshop started with a discussion of the characteristics that are considered important in a good baitfish for tuna fishing. A consensus resulting from the discussion was that while some species could be categorized as "good" baitfish, none of the species examined to date could be considered a "perfect" baitfish. For example, some species may be good at initially attracting the tunas, but may not be too effective in holding the fish at the boat.

In discussing size of baitfish, it was noted that the visual acuity of skipjack tuna and the clear waters of the

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[1] Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

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tropics make it unnecessary for the maximum size of the baitfish to exceed 8 cm. Under most circumstances in tropical waters a baitfish 8-cm long can be detected at 50 m, the usual distance of a fish school from the fishing vessel when chumming is initiated.

A summary of the relative merits of several baitfish species currently used in the Pacific is given in Table 1. The use of a species in an area is generally related to its availability. The effectiveness of the various baitfish species (catch of tuna per unit of baitfish) has not been determined because, while some data are available, there are still too many unknown variables to allow comparisons. In Hawaii, the skipjack tuna catch per pound of baitfish, nehu—*Stolephorus purpureus,* would rank very high due to judicious use of this scarce commodity. In the eastern Pacific where the availability of baitfish is generally not a critical problem, the skipjack tuna catch per pound of northern anchovy, *Engraulis mordax*, or anchoveta, *Cetengraulis mysticetus*, would be considerably lower than the catch rate for Hawaii because of the liberal use of baitfish by the eastern Pacific fishermen.

NATURAL STOCKS

The objectives of the Natural Stocks Session were 1) to evaluate the principal natural baitfish resources of the Pacific with respect to their capacity for supporting local skipjack tuna fisheries and as sources of baitfish for distant-water transport systems, and 2) to recommend specific actions for improving the understanding, development, and management of natural baitfish resources.

Resource Evaluation

Based on available baitfish resource information in the Pacific, areas were described as having 1) known large stocks of baitfish species, 2) limited supplies of baitfish and capable of supporting only localized fisheries, and 3) very little baitfish. In the third category were also areas where information on baitfish is altogether lacking.

In the first group are areas in the Pacific where stocks of anchovies of various species (*Engraulis* spp.) are sufficiently large to support large tuna pole-and-line fisheries. In the eastern Pacific the anchovy and anchoveta found from southern California to Peru have formed the basis for the successful tuna fishery in that region. The annual landings of skipjack tuna in the eastern Pacific fishery ranged from 15,690 to 61,235 t during the period from 1950 to 1960 (before the purse seiners dominated the fishery). In the western Pacific the stocks of *Engraulis japonicus* from coastal waters of Japan currently support Japan's coastal skipjack tuna fishery as well as the recently successful distant southern water tuna fishing operation. The annual Japanese catch of skipjack tuna ranged from 70,428 to 212,985 t from 1960 to 1970. The baitfish stocks in other areas of the western Pacific including Korea, Taiwan, the Philippines, and Australia were believed to be adequate to support any currently existing or projected local skipjack tuna fishery.

A number of the island areas of the central and western Pacific fall into the second category. The principal baitfish species available in these areas belong to the genus *Stolephorus*. Skipjack tuna fisheries in Hawaii, Palau, Papua New Guinea, and the Solomons are examples of localized fisheries.

In Hawaii, the principal baitfish species is the nehu, *Stolephorus purpureus*. The skipjack tuna fishery there is relatively small with total annual landings of less than 5,000 t. The availability of nehu is inadequate for any substantial expansion of the skipjack tuna fishery in Hawaii; thus, increases in the baitfish supply must come from other sources, e.g., cultured species or transport of baitfish from other areas.

The anchovy, *S. heterolobus*, supports a modest skipjack tuna fishery in Palau; the average annual catch was around 4,650 t from 1966 to 1971. A recent study of the baitfish resource indicates that the current harvest of *S. heterolobus* may be approaching the maximum sustainable yield of the stock. Further expansion of the fishery is possible primarily through improved bait handling and usage.

In 1971 the catch of skipjack tuna in the Papua New Guinea fishery amounted to 16,864 t. There appears to be sufficient reason to believe that the *Stolephorus* resources of the area are large enough to support and expand the tuna fishery with current fishing practices. In

Table 1.—Characteristics of various bait species used in the Pacific.

Category	Dussumieridae	*Stolephorus* sp.	Anchovy	Caesiodidae	Apogonidae	Atherinidae	Clupeidae
Survival	Weak	Weak	Medium	Strong	Strong	Strong	Medium
Abundance							
Eastern Pacific	?	Low	High	None	None	High	High
Central Pacific	Low	Moderate	Low	None	Low	Low	Low
Western Pacific	High	High	High	Low	Low	Low	High
Behavior	Good	Good	Good	Good	Good	Poor	Fair
Size (cm)[1]	5	4-6	8-14	4-8	4-5	4-8	8-14
Body form	Elongate	Elongate	Elongate	Elongate	Deep bodied	Elongate	Elongate
Color	Shiny	Shiny	Shiny	Dull	Shiny	Shiny	Shiny
Color pattern	Silvery	Silvery	Silvery	Nonsilvery	Nonsilvery	Silvery	Silvery

[1] Size used as bait.

addition, more effective use of the baitfish resources can be achieved with improved handling and carrying techniques.

In the British Solomons, the stocks of *Stolephorus* presently support a skipjack tuna harvest of 6,000 t. Prospects for expansion are unknown.

The third category includes all other areas where baitfish stocks are known to be very small (e.g., American Samoa), or areas where the available information is too scanty to permit an accurate assessment for skipjack tuna development. Included in this category is Fiji, where a skipjack tuna fishery is in the early stages of development.

Recommendations

In summarizing the discussion on natural stocks of baitfishes, the Session participants developed a set of recommendations for the National Marine Fisheries Service and other organizations interested in baitfish research. The recommendations included:

1. Develop better bait handling and holding techniques to permit fullest utilization of natural baitfish stocks for tuna fishing.
2. Clarify the taxonomic status and nomenclature of the stolephorids and establish a reference collection of specimens.
3. Encourage the exchange of information on research and natural baitfish stocks including unpublished data and trip reports.
4. Adopt the recommendations of the South Pacific Commission's Expert Committee on Tropical Skipjack regarding the collection of standardized baitfish catch statistics, including a measure of nominal baiting effort.

CULTURED BAITFISH SPECIES

From a review of the workshop documents and a discussion based on individual participants' expertise, it was apparent that there is no single baitfish species to solve the problems of all the areas of the Pacific. Nor is there a simple solution to the use of cultured baitfish. Problems faced in culturing baitfish differ markedly from place to place, especially as to the availability of land and fresh water necessary for developing the culture facilities.

In discussing pond culture of baitfishes, a set of general requirements for potential culture species was developed. These included: 1) high reproductive potential, 2) ability to spawn readily in ponds, 3) ability to obtain food low in the food chain, 4) readily handleable and transportable, 5) euryhaline, and 6) lacking spines. Although hardiness is an important factor in the baitfish used in tuna fishing, experience in freshwater baitfish culture work suggests that this characteristic can be developed through proper selective breeding.

Table 2 summarizes the principal characteristics of species that have either been cultured or show culture potential. Highlights of the discussion of these species follow.

Threadfin Shad

This is a euryhaline species which is probably a suitable candidate for polyculture. Threadfin shad, *Dorosoma petenense*, are reported to spawn several times per year, subsist on material low on the food chain, and be fairly economical to raise. Being a euryhaline species, threadfin shad is ideally suited for areas where fresh water is abundant. Unfortunately, for many areas of the Pacific where natural stocks of baitfish are lacking, e.g., most of the tropical islands, fresh water is also a scarce commodity. It was noted that in Hawaii where threadfin shad have been introduced into an agricultural water impoundment system the standing crop of bait-sized threadfin shad during the 1969-70 season was estimated to be 45,454-68,181 kg (100,000-150,000 lb). The reservoir has a surface area of 122 ha at high water and contains approximately 1.14×10^{10} liters of water. The estimated standing crop is equal to approximately 17% to 25% of the baitfish caught in the Hawaiian fishery in 1971.

To date only limited field trials have been conducted using threadfin shad as baitfish for skipjack tuna fishing. Definitive results describing the fishing power of threadfin shad relative to the natural baitfish used in Hawaii are still lacking.

Tilapia

The most extensive field trials using tilapia, *Tilapia mossambica*, as baitfish for tuna fishing have taken place in Hawaii. The results to date have been inconclusive. While the evidence suggests that tilapia may be a suitable substitute baitfish species, in Hawaii it has been generally rejected as such by commercial fishermen. This nonacceptance by fishermen has been attributed to the general conservative nature of fishermen.

Tilapia has the attribute of hardiness and ease in culture. It is conceivable that improvement in fishing success could be achieved by changes in fishing technique.

Mollies

Although cost figures for the culture of various baitfish species are not readily available, the mass-rearing of mollies appears to be the most attractive in terms of economics. An estimate of $2.60/bucket (investigators used 2.7 kg (6 lb)/bucket) was provided as the cost for mollies under a 30,000-bucket annual production system. Favorable characteristics of the mollies include being euryhaline, having the ability to withstand extreme crowding conditions in the baitwells, and having the ability to withstand low oxygen levels. To date the effectiveness of mollies in skipjack tuna fishing has not been demonstrated. While evidence exists that mollies have been used in the past by commercial fishermen in Hawaii

Table 2.—Principal factors of tuna baitfish culture.

Item	Threadfin shad	Tilapia	Mollies	Golden shiner	*Apogon*
Fecundity	14,000-16,000 eggs per female per year. Multiple spawnings	200-800 eggs per female per year (six times per year). 700-1,000 fry survival per female per year	1,600 per female per year	Unknown	Unknown
Hardiness	Satisfactory	Satisfactory	Satisfactory	Satisfactory	Satisfactory
Density tolerance	1,000 lb per acre per year (estimated possible)	Present: 8,000-13,000 lb per acre per year. Estimated: 25,000 lb per acre per year	18,000 lb per acre per year	800-1,600 lb per acre per year (one or two crops)	Unknown
Appearance re traditional bait	Same	Different	Different	Same	Different
Behavior:					
Culture	Satisfactory	Satisfactory	Satisfactory	Satisfactory	Unknown
Used at sea	Satisfactory, but more tests needed	Satisfactory	Inconclusive	Inconclusive	Satisfactory
Ease of culture:					
Intensive	Not established	Good	Good	Not established	Unknown
Extensive	Good	Good	Good	Good	Unknown
Economics	$14 per bucket and 3,660 buckets per acre	$19.58 per bucket with profit; $1.06-1.65 reduced	$2.69 per bucket or $0.45 per pound (@ 30,000 buckets)	$4.00 per pound (air-shipped to Hawaii)	Unknown
Polyculture	Unknown	Unknown	Unknown	Unknown	Unknown
State of the art re mass culture	Not much known	Known	Known	Known	Unknown
Field experiments to date	Inconclusive	Inconclusive	Inconclusive	Inconclusive	Satisfactory
What needs to be done?	1. Project costs, etc. Wahiawa Reservoir 2. Field test	1. Project proposal 2. Field test	1. Hawaii project proposal 2. Hawaii test 3. American Samoa	1. Project costs, etc. 2. Hawaii test	1. Life history research (fecundity)

to catch skipjack tuna, evidence is still lacking that the fishing power of mollies is comparable to that of natural baitfish species, e.g., nehu, in the Hawaiian Islands.

Golden Shiner

Although golden shiner, *Notemigonus crysoleucas*, is strictly a freshwater species and cannot live in seawater, some views were expressed that freshwater species should not be discounted in the search for a suitable baitfish for skipjack tuna fishing. The underlying assumption is that circulation systems can be developed to economically carry freshwater species in baitwells for varying periods of time. The advantages of golden shiner are that the mass culture of this species is well known, they have some of the physical attributes of a good baitfish species, e.g., light coloration, and this species is relatively hardy and withstands mass transport.

To date the golden shiner has not been field tested adequately. The short single test conducted in the Hawaiian Islands was inconclusive.

Apogon

In discussing the suitability of culturing apogons as a baitfish species, the general consensus was that not enough was known about this group to form any definite conclusions.

Since apogons have not been cultured and reared in laboratories to date, the general consensus was that the lack of biological information precludes even a rough estimate of the economics of large-scale culturing systems for these species.

Recommendations

The Session participants recommended the following:

1. Critically analyze future field tests to provide conclusive information on the effectiveness of different baitfish species.
2. Determine the fishing power of the various baitfish species under consideration, using existing data with particular reference to nehu and other *Stolephorus* species as models.
3. Conduct additional field tests with species that have previously shown promise as successful baitfish species, e.g., threadfin shad and golden shiner.
4. Reevaluate the economics of bait production at intervals, using updated cost figures.
5. Recognizing the lack of a "perfect" baitfish species,

continue the search for suitable candidates for cultured baitfish species.

6. Defer work on culture of *Apogon* until studies on critical parameters of this baitfish have been completed, e.g., estimates of fecundity and growth rates.

7. Conduct baitfish extension activities concurrently with the testing of the species in order to overcome problems in fishermen's acceptance of new baitfish species.

TRANSPORTING, HOLDING, AND SUBSTITUTE BAITS

In areas where the supply of natural baitfish stock is lacking or is in very short supply, the several alternatives available to solving the problems include:

1) culturing selected species of baitfish;
2) developing an artificial (substitute) bait; and
3) moving large quantities of baitfish from areas of abundance to areas of scarcity.

Participants of this Session reviewed activities on artificial bait and the transport of baitfish.

A very brief review was made during the Session of previous attempts to attract and hold skipjack tuna schools close to the fishing vessels by using nonliving material. It was noted that some work had been done in Hawaii on the use of dead baitfish, animal extracts, shiny metals, and calcium carbide. While some extracts appeared to create a feeding response by skipjack tuna, none of these responses was of sufficient strength or duration to be promising for commercial fishing application. There has been no work conducted in this field in recent years.

The expansion of the Japanese skipjack tuna fishery to southern waters of the central and western Pacific has been possible because the vessels are able to carry a full load of baitfish from Japan to the fishing grounds. Reports indicate that "aged" anchovy, *Engraulis japonicus*, are carried successfully for 4 wk or more without much mortality.

The attempt by the Honolulu Laboratory (National Marine Fisheries Service) to develop a method of transporting large quantities of northern anchovy from California to Hawaii on commercial freighters was discussed at length. Although the northern anchovy can be carried on baitfishing vessels, it was noted that the commercial roll-on/roll-off freighters represented a possible cost-effective method of transporting baitfish on a continuing basis. The experiment is still in progress and its success could not be predicted at the time.

Special emphasis was placed on the fact that the hardiness of baitfish could be increased substantially by holding the baitfish in pens prior to transporting them. Hardiness appeared to be a key factor in transportation over long distances. If a method of successfully transporting baitfish from one area to another can be developed, the opportunities for an expanded fishery become obvious. The availability of an increased supply of hardy baitfish would mean extending the range of a fishery, providing opportunities for an expansion of fleet size, and increasing the efficiency of tuna fishing by eliminating a major nonfishing activity, i.e., catching of bait.

SUMMARY SESSION

At the Summary Session each chairman reviewed briefly the major findings of his group. The participants then held a general discussion on priorities of future research. Table 3 provides a summary of this discussion.

Table 3.—Three action priorities/alternatives.

	1	2	3
Hawaii	Anchovy transport (Sea Grant, NMFS)	Improve bait handling and utilization (nehu)	Shiners and shad
American Samoa	Mollies (Government of American Samoa)	Economic evaluation of bait transport	—
Trust Territory	*Apogon*	—	—
Other areas	Develop use of natural stocks (availability and accessibility)	Culture suitable species	—

APPENDIX A

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Rapp. P.-v. Réun. Cons. int. Explor. Mer, 170: 223–231. Février 1977.

THE EFFECTS OF INTERNAL WAVES ON FISH SCHOOL MAPPING WITH SONAR IN THE CALIFORNIA CURRENT AREA

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Sonar mapping of schools of fish in surface waters where echo-sounders are ineffective is influenced by changes in the effective range of detection caused by changes in the sound velocity profile as well as by vertical migrations and changes in packing density within the schools.

Analysis has been made of 38 sound velocity profiles over a short period in one region and their variation compared with that in a mass of data for the California area; the short-term variation was of comparable magnitude to that over a 20 year period, with effective detection range varying five-fold. As analysis of the sound velocity profiles at each school mapping station is impractical, a statistical approach is made to determine an 'average' effective detection range. This utilizes historical data, partitions areas and seasons according to intensity of variation in the sound velocity data, allocates sound velocity profiling so as to reduce the standard error of the mean sound velocity gradients in upper waters to a uniform value for all areas and seasons and then, for these profiles, creates a probability diagram for corrections to the number of targets detected at various ranges and depths. An example of the application of the method is given.

INTRODUCTION

Fish school mapping with sonar is a technique developed (Smith, 1970) to study the schools of the northern anchovy, *Engraulis mordax,* which are abundant in the California Current region off the west coast of North America. Sonar mapping provides estimates of the horizontal dimensions of fish schools and an estimate of the number of fish schools and their cross-sectional area per unit area surveyed. This technique was developed because fish schools are frequently found in the upper mixed layer of the ocean where echo-sounders are relatively ineffectual at counting or measuring them. The following difficulties have been noted for echo-sounder surveys for fish schools: (1) These schools may be shallower than the echo-sounder installation or within the zone below the echo-sounder where the outgoing pulsed emission precludes target reception. (2) Biases in estimating the depth, thickness, and compaction of the school may result from the reaction of fish to the approaching ship. (3) The transect of the ship over the school only infrequently coincides with the major or minor axes of the school, thus leading to biased estimates of horizontal school dimensions. (4) Multiple echo returns from near-surface schools may lead to biased estimates of school thickness. The major biases of the sonar mapping technique are changes in effective range of detection caused by changes in packing density within the schools, vertical migration of the schools, and regional, seasonal and short-term changes in the sound velocity profile. However, the range of detection is frequently tens to hundreds of times the width of the echo-sounder beam, and a much larger sample of fish schools is obtained per unit ship time.

Prior to an error evaluation cruise in 1968 (Smith, 1970), it was planned that repetitive temperature profiles would be taken to enable description and analysis to be made of internal waves and their attendant ray tracing profiles in the tidal period part of the internal wave spectrum. The expected tidal period was not as important as internal waves which had shorter periods and higher amplitudes. Relatively coherent time changes were observed at 5-minute intervals. Temporal changes of this order implied spatial changes in the temperature profile which could not reasonably be monitored from a moving ship. Thus, the expense of measuring and analyzing these changes for all fish school mapping surveys appeared prohibitive. An effective range estimate is essential to quantitative surveys, and a statistical approach to the definition of the "average" effective range was sought. The 38 profiles taken for the coherent analysis of the tidal period internal waves were then reanalyzed as though they were independent samples of the effective range in this area. The variability in the temperature and sound velocity gradients in this 3-day example was then

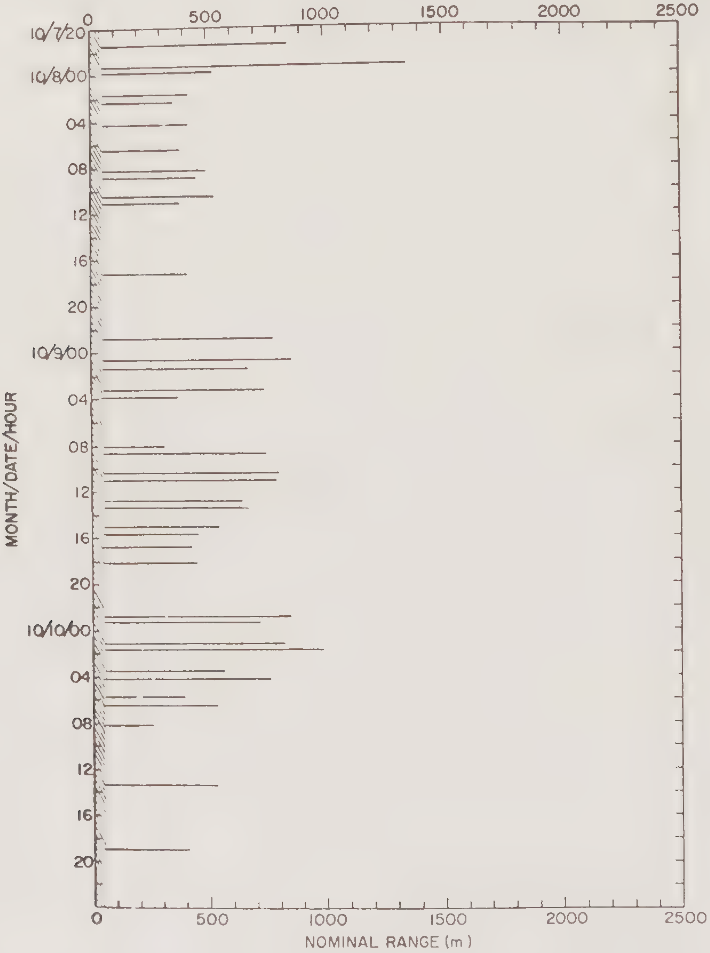

Figure 205. Chronological order of ray trace model derived detection range of − 30 dB sonar target at 20 m depth off Santa Catalina Island, California in October 1968.

compared with the climatic variability in these properties as revealed by long-term records of these properties in this and other regions and seasons.

It is the purpose of this paper to examine the importance and tractability of the internal wave problem with regard to applying unbiased estimates of transmission loss to the description of the probability of target detection by range and depth and the measurement of target strength of those targets received. The analysis and description of the 38 test-temperature profiles will be reported, the variability in thermal and sound velocity profiles will be compared with statistical summaries of hydrographic and bathythermographic measurements taken in California Current area, and a procedure for the allocation of sound velocity estimation effort for an unbiased description of effective sonar range by region and season will be derived.

SOURCES OF DATA

All climatic data were obtained from the archives of the National Oceanographic Data Center of the Environmental Data Service of the National Oceanic and Atmospheric Administration of the United States Department of Commerce. The temperatures, salinities and sound velocities were obtained from approximately 11 000 hydrographic stations at each of 12 depths above 300 m. These include all the stations archived for the area under consideration since 1939. In addition the temperatures were obtained from the 33 183 bathythermograph (BT) profiles taken in this area since 1939 in which temperatures were recorded every 5 m in the upper 45 m. This latter file apparently contains 2·6 % of all BT's ever taken (Couper and LaFond, 1970) and 13·8 % of those taken in the Pacific. A crude attempt to remove the bias of sound velocity calculations from temperature profiles was to apply average salinities by depth, month and year to each of the temperature profiles. Another analysis of the thermal profiles used a constant salinity of 34 ‰.

The rapid sequence expendable bathythermograph (XBT) data were taken by Sippican* equipment from the RV "David Starr Jordan" while underway at ca. 11 knots. The data were digitized manually by 5 m inter-

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* This does not constitute endorsement of this commercial product by the U.S. Government.

Table 44. Sound velocity profiles (m sec^{-1}) evaluated for range of detection of – 30 dB sonar target at 20 m depth

Short range

Depth m	Time 0812 Range 256 m	Time 0806 Range 311 m	Time 0222 Range 357 m	Time 0351 Range 375 m	Time 0630 Range 384 m	Time 1106 Range 384 m	Time 0543 Range 393 m	Time 1712 Range 411 m	Time 1856 Range 411 m	Time 0143 Range 421 m	Time 0419 Range 421 m	Time 1650 Range 430 m	Time 1809 Range 448 m
0	1517·0	1516·2	1517·0	1519·3	1517·0	1517·9	1516·7	1517·9	1516·7	1517·9	1517·9	1518·7	1518·7
5	1515·1	1515·1	1516·3	1517·4	1516·5	1516·3	1516·3	1516·5	1516·3	1516·5	1516·8	1517·4	1517·7
10	1505·8	1509·0	1511·2	1516·0	1510·5	1515·2	1510·5	1516·0	1512·1	1516·0	1516·0	1516·6	1516·6
15	1502·6	1501·6	1508·1	1513·4	1505·9	1510·6	1507·4	1507·4	1507·1	1507·4	1507·4	1513·1	1513·7
20	1501·1	1500·1	1504·6	1509·1	1503·7	1505·9	1503·3	1504·0	1504·0	1505·6	1501·7	1505·9	1509·1
25	1500·5	1499·8	1502·8	1507·6	1499·5	1502·8	1501·1	1501·1	1502·8	1501·8	1498·8	1503·7	1504·4
30	1497·9	1498·2	1501·2	1503·5	1497·9	1500·2	1500·2	1499·2	1500·9	1501·5	1498·9	1501·5	1502·2
35	1497·3	1497·6	1497·3	1501·3	1497·3	1498·0	1498·0	1497·6	1498·3	1499·6	1498·6	1500·3	1499·3
40	1497·4	1495·7	1496·4	1499·7	1495·7	1497·7	1497·7	1496·0	1497·7	1499·4	1497·4	1499·0	1497·7
45	1495·4	1495·1	1495·1	1498·1	1495·5	1497·1	1495·1	1495·1	1496·1	1497·5	1495·4	1497·1	1495·8
50	1494·8	1494·1	1493·4	1495·9	1495·2	1495·5	1493·4	1494·5	1494·5	1495·2	1495·2	1495·9	1494·5
70	1491·3	1491·3	1491·0	1491·7	1491·7	1492·0	1491·3	1491·3	1491·0	1492·4	1491·7	1492·7	1490·6
90	1490·0	1490·0	1490·3	1490·9	1490·0	1490·9	1490·0	1490·3	1489·7	1490·3	1489·3	1490·0	1489·7
110	1489·7	1490·0	1490·0	1490·6	1489·7	1490·6	1490·0	1489·7	1489·0	1490·0	1489·3	1489·7	1489·7
130	1490·0	1489·6	1490·0	1490·3	1489·6	1490·3	1489·0	1489·0	1488·7	1490·0	1489·0	1489·6	1489·6
150	1490·0	1489·3	1490·0	1490·3	1489·6	1489·6	1489·0	1489·0	1489·3	1489·6	1488·7	1490·0	1489·3

Medium range

Depth m	Time 0850 Range 457 m	Time 1544 Range 457 m	Time 0817 Range 494 m	Time 2349 Range 521 m	Time 1033 Range 530 m	Time 1325 Range 530 m	Time 0627 Range 539 m	Time 1503 Range 549 m	Time 0332 Range 558 m	Time 1246 Range 649 m	Time 0121 Range 677 m	Time 1321 Range 686 m	Time 2318 Range 722 m
0	1516·5	1518·5	1516·7	1516·5	1518·7	1517·9	1516·2	1517·3	1516·7	1517·9	1517·0	1518·2	1517·0
5	1516·0	1517·4	1516·5	1516·0	1517·1	1516·5	1516·3	1516·3	1516·5	1516·5	1516·5	1517·1	1516·8
10	1514·0	1516·6	1510·5	1511·9	1516·9	1516·6	1509·0	1516·0	1513·3	1516·3	1516·3	1516·9	1516·3
15	1505·9	1512·8	1504·2	1510·0	1516·4	1512·2	1505·9	1513·7	1510·0	1516·1	1513·7	1516·7	1510·9
20	1504·0	1507·2	1499·1	1508·2	1512·3	1508·5	1503·0	1510·7	1508·2	1515·9	1510·4	1516·2	1505·9
25	1500·1	1505·0	1498·5	1503·7	1507·6	1502·8	1501·8	1504·4	1506·0	1510·8	1503·7	1506·0	1502·8
30	1500·2	1501·9	1496·9	1501·9	1503·8	1500·6	1499·2	1500·6	1501·5	1504·5	1501·5	1502·2	1499·6
35	1497·3	1499·3	1495·3	1498·6	1500·3	1499·3	1497·0	1498·3	1498·6	1501·3	1499·0	1499·3	1498·0
40	1496·7	1497·7	1495·0	1497·7	1499·0	1499·0	1496·0	1497·7	1497·0	1499·7	1497·0	1498·1	1497·0
45	1495·1	1497·1	1494·0	1496·8	1497·1	1497·5	1494·7	1495·8	1495·4	1497·8	1495·4	1497·1	1496·5
50	1494·8	1496·2	1493·4	1495·5	1495·9	1496·9	1493·8	1495·2	1493·8	1496·5	1494·5	1495·5	1495·2
70	1491·3	1492·4	1491·7	1492·0	1493·8	1492·0	1490·6	1492·0	1491·0	1492·4	1490·6	1490·6	1492·9
90	1489·7	1490·6	1490·3	1490·6	1490·9	1490·3	1489·7	1490·6	1490·0	1490·3	1490·3	1490·0	1490·0
110	1489·3	1490·0	1490·0	1490·3	1490·3	1489·7	1489·3	1489·7	1489·3	1489·7	1490·3	1489·7	1489·7
130	1488·7	1490·0	1489·6	1490·0	1490·0	1489·6	1489·6	1490·0	1489·0	1489·6	1490·0	1489·6	1489·3
150	1488·7	1490·3	1489·0	1489·6	1490·0	1489·6	1490·0	1489·3	1489·3	1489·6	1490·3	1490·0	1489·6

(To be continued.)

Table 44 (continued).

Long range

Depth m	Time 0312 Range 741 m	Time 0839 Range 750 m	Time 0409 Range 759 m	Time 2250 Range 777 m	Time 1057 Range 796 m	Time 1025 Range 805 m	Time 0109 Range 823 m	Time 2129 Range 850 m	Time 2248 m Range 850 m	Time 0041 Range 860 m	Time 0144 Range 988 m	Time 2315 Range 1344 m
0	1517·0	1517·0	1516·2	1517·3	1516·5	1516·5	1516·5	1516·7	1517·0	1517·9	1517·0	1516·5
5	1516·5	1517·1	1516·3	1517·1	1516·3	1516·3	1516·3	1516·3	1516·3	1517·4	1517·1	1516·3
10	1516·3	1516·3	1515·2	1516·6	1516·0	1516·3	1516·0	1516·3	1516·3	1517·5	1517·2	1516·3
15	1515·6	1511·2	1507·4	1514·3	1510·6	1515·0	1515·8	1516·4	1516·1	1516·7	1517·3	1516·4
20	1510·7	1506·9	1505·6	1512·3	1504·3	1504·0	1509·1	1510·7	1512·0	1515·0	1516·8	1516·5
25	1503·7	1504·1	1501·1	1504·4	1501·1	1502·8	1503·4	1502·8	1508·6	1506·0	1514·5	1510·8
30	1501·2	1501·2	1498·2	1500·9	1499·9	1501·2	1499·9	1501·2	1502·9	1500·6	1507·7	1506·4
35	1500·3	1498·6	1496·3	1499·6	1498·6	1499·0	1498·6	1498·0	1500·3	1499·6	1502·0	1501·3
40	1498·7	1498·4	1495·7	1498·4	1497·4	1498·1	1497·7	1497·0	1499·4	1498·1	1499·4	1498·7
45	1496·5	1497·1	1494·7	1497·5	1496·8	1496·1	1495·4	1495·4	1499·1	1496·5	1497·5	1496·5
50	1495·5	1496·5	1493·8	1495·2	1495·5	1495·9	1495·2	1495·2	1495·2	1495·2	1496·2	1494·5
70	1492·4	1494·8	1490·6	1491·7	1492·7	1494·1	1492·0	1491·3	1491·7	1492·4	1492·0	1491·3
90	1490·3	1492·7	1489·7	1490·6	1490·9	1492·3	1490·0	1491·6	1490·0	1491·6	1490·6	1490·3
110	1490·0	1492·3	1489·7	1490·6	1490·3	1492·0	1490·0	1493·4	1490·0	1491·2	1490·3	1490·0
130	1489·6	1492·3	1489·6	1490·6	1490·0	1491·9	1489·6	1494·7	1489·0	1491·3	1490·3	1489·6
150	1489·6	1492·6	1490·0	1490·3	1490·3	1491·6	1489·6	1494·0	1489·6	1491·3	1490·6	1490·0

vals from the surface to 50 m and by 20 m intervals from 50 to 450 m. Characteristic salinities were taken from a T-S diagram for this area and season.

METHODS OF ANALYSIS

The ray tracing program was operated by the Ocean Operations Project of the U.S. Navy Fleet Numerical Weather Central, Monterey, California. Parameters of the program included a source depth of 3·65 m, target depths of 4, 10, 20, and 50 m, source frequencies of 11, 29·8, and 75 kHz, arbitrary surface and bottom characterizations, and stepping angles of 0·2° from 0·02° to 14·76° down and 0·05° from 15·00° to 30·00° down, with a transducer which is 10° between the 3 dB down points and declined downwards 4° from the surface. Estimates of transmission loss to the four target depths were reported in 10 yard intervals to a point that exceeded the combined threshold specified by minimum target strength (—30 dB), receiver sensitivity, source level, and attenuation. Transmission loss variations were evaluated at 29·8 kHz, for targets at 20 m depth, at ranges of 250 and 300 m.

Table 45. Mean gradients ($m_x \sec^{-1} m_z^{-1}$) for the sound velocity profiles in the upper 30 m

Depth (m)	Detection range		
	Short	Medium	Long
0	– 0·2	– 0·1	– 0·0
5	– 0·7	– 0·3	– 0·1
10	– 1·0	– 0·6	– 0·4
15	– 0·7	– 0·6	– 0·8
20	– 0·5	– 0·9	– 1·0
25	– 0·4	– 0·6	– 0·7
30	– 0·4	– 0·5	– 0·5

RESULTS

The data were examined to determine the effects of transmission loss variations on target detection. The maximum range of detection varied from 256 to 1344 m in the 38 ray trace analyses. There were modes at detection ranges of 400 and 800 m. These detection ranges are illustrated in chronological order in Figure 205. The detection range at a target depth of 20 m has been used for an index of effective range. In Table 44 the thermal profiles are listed in increasing order of the effective range and are arbitrarily divided into short range (< 450 m), medium range (450—750 m), and long range (> 750 m). The variation in detection range is apparently caused by changes taking place in the thermal profile in the upper 30 m. For all three range categories the mean slope for the sound velocity profile is 0·5 metres per second per metre depth ($m_x \sec^{-1} m_z^{-1}$) between the surface and 35 m. It is apparent from Table 45 that the differences are caused by the distribution and intensity of the gradients in the upper layer.

To see whether this series of thermal profile samples taken in October of 1968 is representative of the kinds

Table 46. Statistical summary of sound velocity and sound velocity gradient profiles and comparison between October 1968 and long-term regional profiles in October; sound velocity in m/s, and sound gradient in m/s/m depth

Depth m	Short term					Long term			
	Sound velocity		Sound gradient			Sound velocity		Sound gradient	
	$\bar{X}$	S	$\bar{X}$	S	s.e.$\bar{X}$	$\bar{X}$	S	$\bar{X}$	S
0	1517·3	0·82	– 0·1426	0·117	0·019	1515·7	4·48	– 0·1170	0·201
5	1516·6	0·56	– 0·3558	0·500	0·081				
10	1514·8	2·83	– 0·7042	0·544	0·088	1514·6	5·17	– 0·4483	0·352
15	1511·3	4·42	– 0·7158	0·446	0·072				
20	1507·9	5·02	– 0·7816	0·488	0·079	1510·0	5·94	– 0·4993	0·277
25	1503·8	3·44	– 0·5484	0·324	0·053				
30	1501·0	2·20	– 0·4458	0·235	0·038	1505·0	6·20	– 0·3487	0·148
35	1498·8	1·45	– 0·2221	0·128	0·021				
40	1497·7	1·22	– 0·2858	0·123	0·020				
45	1496·3	1·13	– 0·2347	0·150	0·024				
50	1495·1	0·90	– 0·1629	0·038	0·006	1497·9	4·78	– 0·1633	0·095
70	1491·8	0·94	– 0·0700	0·032	0·005				
75						1493·7	3·42	– 0·0922	0·069
90	1490·4	0·71	– 0·0146	0·022	0·004				
100						1491·4	2·61	– 0·0439	0·041
110	1490·1	0·86	– 0·0091	0·019	0·003				
125						1490·3	2·29	– 0·0298	0·029
130	1490·0	1·09	0·0004	0·018	0·003				
150	1490·0	1·02	0·0041	0·018	0·003	1489·5	2·22	– 0·0173	0·019

of gradients to be expected in this area at this season, the average profile for the 38 samples in 1968 is compared with the long-term average for all profiles taken in hydrographic casts in this area in October since 1939 (Table 46). Both the sound velocities and the sound velocity gradients are within the expected range.

In a consideration of the effects of transmission loss variations on target strength determination, the data

Table 47. Variations in transmission loss

Time	20 m range (m)	250 m Transmis. loss A (dB km^{-1})	300 m Transmis. loss B (dB km^{-1})	A to B Transmis. loss C (dB km^{-1})
		Short		
0812	256	204	–	–
0806	311	206	181	65
0222	357	201	178	75
0351	375	196	168	43
0630	384	206	182	75
1106	384	197	170	48
0543	393	204	182	83
1712	411	202	175	52
1856	411	201	179	79
0143	421	201	173	45
0419	421	204	176	53
1650	430	200	172	46
1809	448	197	171	49
		Medium		
0850	457	201	176	65
1544	457	199	172	54
0817	494	210	188	86
2349	521	198	170	48
1033	530	195	169	50
1325	530	199	172	50
0627	539	208	189	100
1503	549	196	169	46
0332	558	197	173	65
1246	649	193	163	31
0121	677	197	171	55
1321	686	195	166	36
2318	722	201	176	60
0312	741	197	171	54
		Long		
0839	750	201	175	60
0409	759	201	176	65
2250	777	196	169	48
1057	796	204	177	57
1025	805	204	177	53
0109	823	200	173	56
2129	850	199	172	50
2248	850	197	171	56
0041	860	195	167	39
0144	988	194	166	39
2315	1344	193	163	31

Table 48. Bathythermograph-derived maximum standard deviation of sound velocity gradient (m_x sec^{-1} m_z^{-1}) in the upper 30 m by region and month

Month/Region	CCI	CCO	SCI	SCO	SCS	BCI	BCO	BCS	SBI	SBO
Jan	0·08	0·10	0·16	0·14	0·08	0·15	0·09	0·06	0·21	0·06
Feb	0·08	0·09	0·13	0·10	0·06	0·14	0·14	0·07	0·14	0·07
Mar	0·15	0·08	0·18	0·12	0·07	0·15	0·08	0·10	0·18	0·12
Apr	0·31	0·14	0·27	0·16	0·08	0·23	0·09	0·10	0·24	0·10
May	0·21	0·17	0·35	0·20	0·19	0·28	0·18	0·18	0·28	0·14
Jun	0·25	0·26	0·48	0·29	0·19	0·35	0·17	0·13	0·31	0·32
Jul	0·46	0·31	0·56	0·36	0·26	0·43	0·26	0·16	0·67	0·44
Aug	0·30	0·46	0·58	0·42	0·29	0·44	0·40	0·30	0·61	0·53
Sep	0·38	0·44	0·50	0·45	0·39	0·40	0·48	0·39	0·45	0·48
Oct	0·35	0·66	0·54	0·43	0·34	0·38	0·32	0·19	0·47	0·67
Nov	0·27	0·35	0·36	0·32	0·21	0·36	0·39	0·28	0·55	0·73
Dec	0·16	0·34	0·31	0·20	0·15	0·31	0·05	0·05	0·38	0·49

were also examined to determine the magnitude of variation to be expected in short-range transmission loss. The data in Table 47 are expressed in dB per kilometre for easy comparison. There appears to be very little difference at these ranges, for example, the total variation attributable to transmission loss between the ship and the target at 20 m depth and 250 m range is only over a 4·3 dB range for 38 observations. By 300 m range the variation has reached 7·8 dB. As target strength for schools in this region appears to vary by approximately 30 dB (Smith, unpublished data; Holliday, MS), the variation in this example does not seem to be large.

DISCUSSION

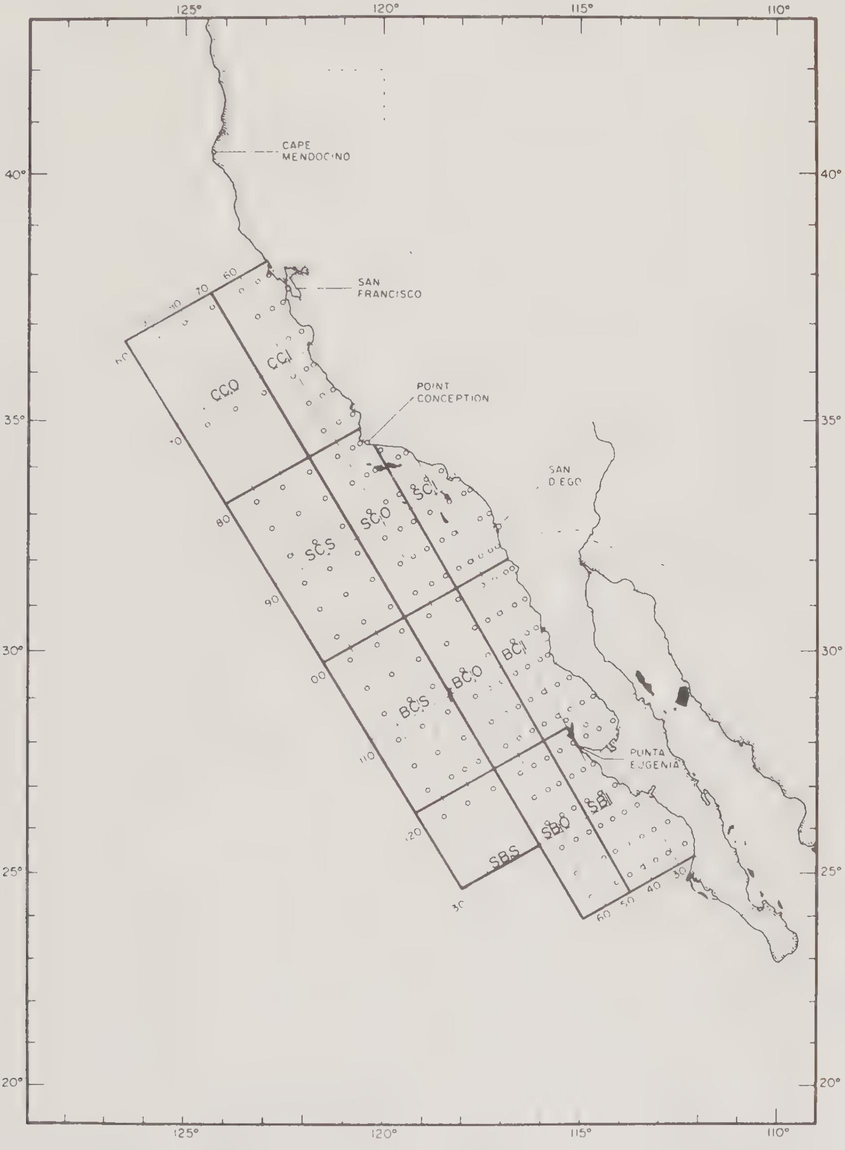
It appears from the above results that the most important effect of internal waves on fish school mapping with sonar is the variation of detection range. In one 3-day period at one 2·4 nautical mile grid, the effective range varied fivefold (Fig. 205). The magnitude of the sound velocity changes in this relatively short interval is comparable to the full range of changes in this month in this area for a 20 year climatic record. Since the precision of estimates of the effective sonar range may control the precision of estimate of the number of targets per unit area, it is imperative that an unbiased and current estimate of effective range be sought.

It would appear from these sample profiles that the estimate of target strength is not as susceptible to short-term changes as is range. As the targets are detected, measured and passed at 11–12 knots and as the usual target is less than 50 m wide (Smith, 1970), the variation in half-minute period would appear to be a relatively minor problem.

The brief field study reported above was an attempt to gain a direct measurement of internal waves at the tidal period. The results indicate that internal waves of shorter period are important sources of variation. The expense of "real-time" collection and analysis of

Table 49. An allocation of sound velocity profiles among regions and months to equalize the standard error of the maximum sound velocity gradient in the upper 30 m

Month/Region	CCI	CCO	SCI	SCO	SCS	BCI	BCO	BCS	SBI	SBO	Total
Jan	2	2	2	2	2	2	2	2	3	2	21
Feb	2	2	2	2	2	2	2	2	2	2	20
Mar	2	2	2	2	2	2	2	2	2	2	20
Apr	8	2	6	2	2	4	2	2	5	2	35
May	3	2	10	3	3	6	2	2	6	2	39
Jun	5	6	18	6	3	10	2	2	8	8	68
Jul	17	8	25	10	6	14	6	2	36	15	139
Aug	7	17	27	14	6	15	13	7	29	22	157
Sep	11	15	20	16	12	13	18	12	16	18	151
Oct	10	35	23	14	10	11	8	3	17	36	167
Nov	6	10	10	8	3	10	12	6	24	42	131
Dec	2	10	8	3	2	8	2	2	11	19	67
Total	75	111	153	82	53	97	71	44	159	170	1015


125°
120°
115°
110°
40°
35°
30°
25°
20°
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
CC,O
CC,I
SC,S
SC,O
SC,I
BC,S
BC,O
BC,I
SB,S
SB,O
SB,I
60
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120
130
40
30
50
60

Figure 206. Regional boundaries for allocation of real-time sound velocity profiling effort. Code letters are: CC = Central California, SC = Southern California, BC = Baja California, SB = South Baja, I = Inshore, O = Offshore, and S = Seaward. The South Baja Seaward region was inadequately sampled to provide monthly profiling needs.

coherent sound velocity profiles and estimation of their resultant transmission loss appears to be prohibitive: a statistical approach is necessary.

EFFICIENT CHARACTERIZATION AND EVALUATION OF SONAR TRANSECTS

The aim here is to devise a method for the most effective overall reduction in variability in the description of effective sonar range, in space and time, using climatic data. The following steps need to be taken for a first approximation:

1) assemble historical thermal or sound velocity data by region and season;
2) partition regions and seasons by intensity of variation:

Table 50. Sonar limiting ray table

Time	Target depth (m)	Near limit (m)	Far limit (m)	Time	Target depth (m)	Near limit (m)	Far limit (m)
0351........	4	9	55	0817........	4	9	146
	10	18	238		10	18	411
	20	37	375		20	37	494
	50	82	585		50	82	677
1650........	4	9	64	1321........	4	9	73
	10	18	293		10	18	366
	20	37	430		20	37	686
	50	82	622		50	82	786

3) allocate the real-time sound velocity profiling activity among regions and seasons to reduce the standard error of the mean sound velocity gradient in the upper 30 m to a uniform value for all regions and seasons; and
4) from these real-time measurements of sound velocity, create a probability diagram to apply corrections to the numbers of targets received at various ranges and depths.

An example of this approach may be seen by reference to Tables 48 and 49. In Table 48 the long-term maximum standard deviation of the sound velocity gradient in the upper 30 m is arranged by month and region. The regions (illustrated in Fig. 206) are denoted by code letters, the first two letters of which refer to the name of a coastal section (CC = Central California; SC = Southern California; BC = Baja California; SB = South Baja) and the last letter refers to dis-

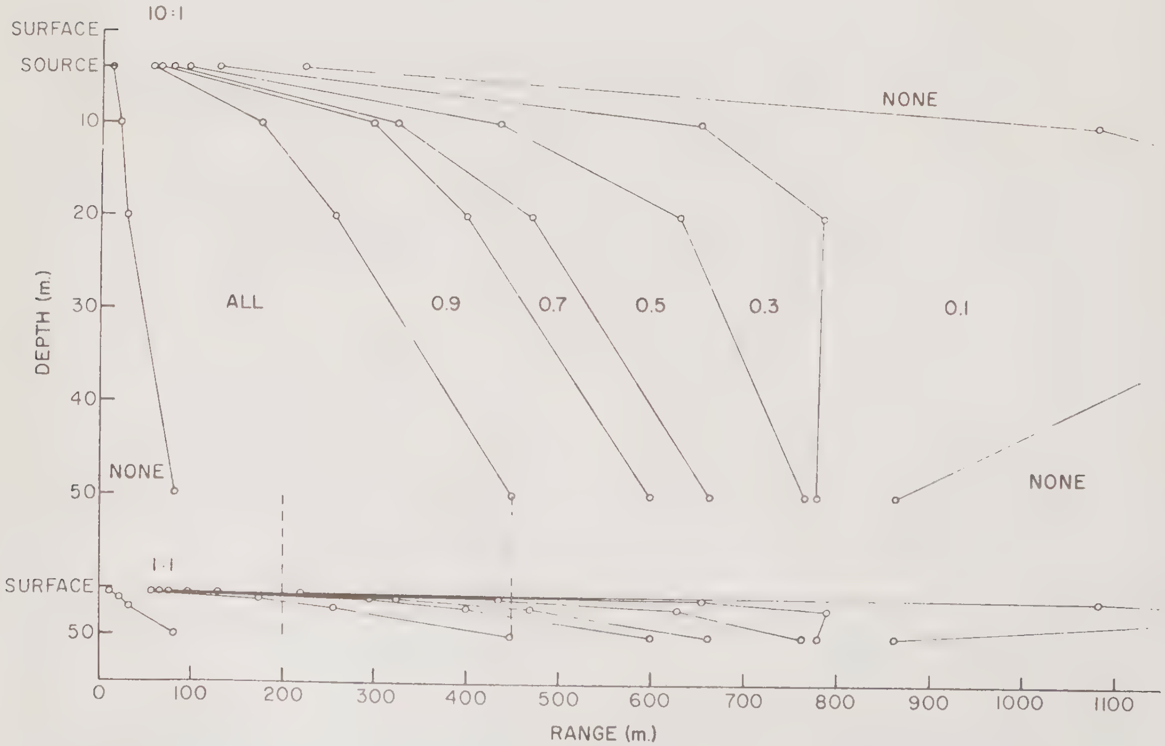

Figure 207. A pooled summary of 38 range trace analyses of limiting range by depth, contoured by the probability of detection of − 30 dB targets.

tance from the coast (I = Inshore, 0–80 miles; O = Offshore, 80–160 miles; S = Seaward, 160–280 miles). The table values are of the maximum standard deviations in sound velocity gradients expressed as m_x sec^{-1} m_z^{-1} in 5-metre intervals in the upper 30 m. The standard error of a group mean is obtained by dividing the standard deviation by the square root of the number within the group. Conversely, one may specify the number of profiles necessary to reduce the standard error of the group mean to a pre-set level by solving for N:

$$N_{ij} = \left(\frac{S_{ij}}{\text{s.e.}}\right)^2$$

where N_{ij} is the number of observations in the ith region in the jth month, S_{ij} is the maximum standard deviation of sound velocity gradient in the month/region stratum in the upper 30 m, and s.e. is the predetermined level of the standard error (ca. 0·1 m_x sec$^{-1}m_z^{-1}$ for this example.

For the purpose of this example, it was assumed that no fewer than two thermal profiles per month/region stratum would be taken. Roughly 1000 thermal or sound velocity profiles were allocated to an entire year for this example. The number of sound velocity profiles specified is reported by month and region in Table 49. It is interesting to note that the climatically derived number of profiles required for the Southern California Inshore region (SCI) in October is 23. This number of profiles would have reduced the standard error of the 10–15 m sound velocity gradient to 0·1 m_x sec^{-1} m_z^{-1} (see Table 46).

PROBABILITY DIAGRAM

The technique for pooling the sound velocity profiles in order to obtain an unbiased estimate of the water insonified by range and depth along a sonar transect, involves use of a probability diagram. The first step is to define the limiting rays for each sound velocity profile near to and remote from the ship for each target depth, given the parameters of the sonar equation. The ranges are next ordered for each target depth and probability levels are interpolated for each target depth. The array of probabilities is then contoured.

To illustrate the technique, four limiting ray calculations at four target depths have been chosen at random from the set of 38 reported above (Table 50). The limiting rays at each target depth are then ordered and interpolated ranges are calculated for probabilities of 0·75, 0·50 and 0·25 for example, and the resulting chart would be contoured at these values. An example of results for all 38 ray trace analyses is provided in Figure 207. The upper diagram is exaggerated vertically to show detail and the lower diagram is drawn on a 1:1 basis.

CONCLUSION

With respect to internal waves and the allocation of sound velocity profiling effort, two directions of research are recommended. One is to explore the optimum depth of placement of the sonar transducer with respect to internal waves and the sound velocity profile so as to minimize the shadow zones and their variation with time. The other is to explore the further allocation of sound velocity profiling effort according to the incidence of fish schools by region and by month.

ACKNOWLEDGEMENTS

The interdisciplinary nature of this research has required the counsel and direct assistance of many people over the past years. Among these have been the Captain and men of the RV "David Starr Jordan"; Drs W. H. Lenarz and C. O'Connell, J. Zweifel, T. Saur, and other colleagues at the Southwest Fisheries Center; Professors J. D. Isaacs, F. N. Spiess, V. C. Anderson, and Ms. M. Robinson of the University of California, Scripps Institution of Oceanography at San Diego: Captain P. M. Wolff, Captain S. Houston, Lt. Cdr. J. Bridenstein, T. Laevastu, Drs G. LaFond and E. Barham, and I. E. Davies and W. Batzler of the U.S. Navy; Dr T. Austin and H. Odum of the NOAA Environmental Data Service; J. Johnson of the NMFS Pacific Environmental Group; the research and training staff of Simrad in Horten, Norway, and F. Devold, L. Midttun, and O. Nakken of the Inst. Mar. Res. Bergen. The responsibility for errors and faults in interpretation of these data lie solely with the author. Technical and numerical assistance was received from Nancy Wiley, R. C. Counts, Esther Barker, and J. Thrailkill.

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7749

FAO Fisheries Technical Paper No. 175 FIR/T175(En)

STANDARD TECHNIQUES FOR PELAGIC FISH EGG AND LARVA SURVEYS

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FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS
Rome, December 1977

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M-43
ISBN 92-5-100515-X

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PREPARATION OF THIS PAPER

This publication is one of a series of FAO manuals in fisheries science. It has been prepared as part of the programme of the Fishery Resources and Environment Division and is largely based on the work of a Working Party on Fish Egg and Larval Surveys established following the recommendation of the Fourth and Fifth Sessions of the FAO Advisory Committee on Marine Resources Research.

Through a contract awarded to the Southwest Fisheries Center, National Marine Fisheries Service, La Jolla, California, the present version of the manual was prepared by Paul E. Smith and Sally L. Richardson.

The manual will be primarily for use in FAO field projects and training courses, and by national institutions, especially in developing countries, which may be conducting fish egg and larval survey programmes. The final edition of the paper in the official languages of FAO will eventually be published incorporating any revisions that may be proposed by the users of the manual.

Distribution

FAO Department of Fisheries
FAO Regional Fishery Officers
Selector SM
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Bibliographic reference

Smith, P.E. & S. Richardson (1977)
FAO Fish.Tech.Pap., (175):100 p.
Standard techniques for pelagic fish
egg and larval surveys

Ichthyoplankton surveys. Methodology.
Sampling (biological). Plankton
collecting devices. Stock assessment.

PREFACE

A Working Party on Fish Egg and Larval Surveys was established in 1968 following the recommendation of the fourth and fifth sessions of the FAO Advisory Committee on Marine Resources Research (ACMRR), whose terms of reference included the preparation of a Manual (field guide) for this aspect of fishery science. The contributions prepared by the Working Party members mainly based on the discussions of the Working Party held in Tunis from 22 to 27 October 1969 and on further advice provided by ACMRR during its Sixth Session, were recently edited by Prof. G. Hempel, and published by FAO: Fish Egg and Larval Surveys (Contributions to a Manual) (FAO Fish.Tech.Pap., 122). This provisional version has been produced for use as a background document during the first International Training Course on Fish Egg and Larval Studies, held in La Jolla from 2 to 29 September 1973 (see FAO.Fish. Rep., 144). Based on the experience gained during the course and taking into account the recommendation of the ACMRR that the Manual should provide a review of the circumstances under which egg and larval surveys are more appropriate and cost-effective than other field surveys, the provisional version was edited and supplemented in order to provide the potential new users of this survey technique with a balanced view of its value and limitations as well as of cost effectiveness.

Many people have been generous with their time and thought to make this manual possible. The consistent support and encouragement of Dr. Elda Fagetti has been the essential energy behind this work and the advice and urging of Dr. Gotthilf Hempel and Dr. Elbert Ahlstrom have guided the production of the manual. The authors of a precursor to this manual (Hempel, 1973), E.H. Ahlstrom, J.M. Colebrook, E. Fagetti, G. Hempel, K. Sherman, S. Tanaka have furnished major sections of text within this edition. Much of the procedural information in section 2 has been derived from procedural description (Kramer et al, 1972) relative to the CalCOFI surveys. Significant editing was offered by Dr. William Richards, Dr. William Aron, Dr. William Lenarz, and Mr. David Kramer. Helpful comments were received from Dr. J.D. de Ciechomski, M.E. Diaz, Dr. J.A. Gulland, Dr. J. Kinzer, Dr. R. Lasker, Dr. A. Longhurst, R. Marak, B. Monsalve, Dr. W. Nellen, M.A. Padilla, A.M.Perez-Franco, Dr. B.J. Rothschild, Dr. M. Ruivo, Dr. D. Sahrhage, Dr. H. Santander, Mr. K. Sherman, Dr. A.C. Simpson, Dr. M. Vanucci, and K. Venkataramaniyam. Administrative assistance was received from Dr. E.F. Akyüz, Mr. Ben Remington, Mr. I. Barrett, Mr. Richard Schwartzlose and Ms. Barbara Rowe. Technical assistance was received from K. Akutagawa, F. Crowe, S. HuFei, E. Stevens and J. Thrailkill and typing was by Janica Scott. Dr. Sally Richardson incorporated the comments and reviews, unified the style of the text, and rewrote major sections and she has been named assistant editor for this manual.

Paul E. Smith

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1. Introduction

The purpose of this manual is to describe the techniques necessary for conducting quantitative ichthyoplankton surveys. The main focus of the description will be directed toward the use of such surveys for estimating the spawning biomass of pelagic fishes. However, ichthyoplankton surveys have many other uses (Table 1.1) some of which will also be taken into account within the framework of the text, especially those dealing with detection and appraisal of fishery resources.

1.1. Background

Data on the size of the stock, together with an index of its productivity, are essential to understand the dynamics of an exploited fish stock and to evaluate the effect of fishing on the stock so as to manage the fishery. These indices are usually derived from life history data and statistics of total catch. Various methods have been developed to produce estimates of absolute or relative size of stocks. These methods include:

(i) analysis of catch and effort statistics,

(ii) tagging experiments,

(iii) observation or direct counting,

(iv) sonic surveys,

(v) surveys of eggs and larvae

Under certain conditions, each of the methods may provide a reliable estimate of the size of stocks. There are, however, considerable limitations to the application and accuracy of each of the methods. Therefore, whenever possible, more than one independent estimate should be attempted.

In most cases, much information on stocks is obtained through commercial fisheries which involve various sources of bias. Hence estimates of stock size made independently of the commercial fisheries are very useful. Among the methods listed above, the first two depend much upon commercial fisheries whereas the other three are largely independent of fisheries.

Catch and effort data analysis has been applied to many commercially exploited fish stocks. Whenever possible, this method should be attempted for stock analysis. An advantage of this method is that the basic data for the study are often available without special surveys or with a small amount of additional work. As catch and effort data are needed for many purposes including administrative requirements, surveys for them are conducted as government routine in many countries. Schaefer (1957) and Silliman (1967) provide good examples of catch and effort data analysis with a simple model of population dynamics.

In order to apply a more detailed model, such as that proposed by Beverton and Holt (1957), age specific data (e.g., growth of fish, and age structure in the catch as well as detailed catch and effort statistics classified by areas and seasons) are needed. Collecting these data requires some care but generally the work is not quite as costly as that required for surveys at sea.

One of the most serious limitations of this method is introduced by rapid changes in gear efficiency which are now going on everywhere in the world fisheries. Catch per unit effort will give erroneous patterns of the change in abundance if estimates of major long-term changes in the efficiency of gear are lacking.

Other difficulties include changes in availability and vulnerability related to fish ecology and oceanographic conditions. These changes will seriously affect the landings and catch per unit effort, resulting in imprecise information on the size of the stock and the mortality rates. This is particularly true for swiftly moving pelagic fishes.

Mortality analysis with the catch and effort data is difficult to apply to a fish species with a short life span, or to a stock exploited by several types of gear each specialized for capturing different developmental stages of fish.

Furthermore, detailed and reliable statistics on catch and effort are not always available to fishery scientists and the available data do not necessarily represent the stock because fisheries are often biased by their economic interest.

Tagging fish is a very useful method for estimating abundance and has been used widely for stock analysis (e.g., ICNAF, 1963). In many cases, this method has provided reliable estimates of the size of stock. However, there are many limitations. Differential mortality sometimes makes the application of this method impossible. This is particularly true for small sized fish such as sardine and anchovy or small juveniles. Recovery rate from the catch and reporting rate by fishermen may be considerably lower than unity for the catch treated in mass. Tag shedding and non-random distribution of tagged fish in the stock are among many factors which introduce error and bias in the estimates. Cost of fish for release is sometimes exceedingly high, if a large enough number are to be released for a reliable estimate.

Direct counting by eye can be applied only for large sized fish. The number of schools of fish such as sardine could be counted but this would be performed much better by acoustic instruments.

Table 1.1. On the use of ichthyoplankton surveys. (From Hempel, 1973)

Detection and appraisal of fishery resources

Exploring for new resources

Locating spawning concentrations of important stocks

Describing relative abundances of commercially important stocks; comparison within and amongst regions

Monitoring long-term changes in the composition and abundance of resources and in spawning times and areas

Studies in biology and systematics

Studying the development, growth, behaviour, food requirements and mortality of the early stages of economically important fishes as related to environmental factors

Providing a better understanding of oceanic biology, e.g., zoogeography and ecology of all organisms in the samples

Clarifying fish systematics

Studies in population dynamics of fishes

Tracing fluctuations in spawning stocks by estimating the abundance of their eggs and young larvae

Forecasting year-class strength on the basis of the abundance of older larvae

Estimating abundance of a stock based on its spawning production

Discriminating between stocks of the same species

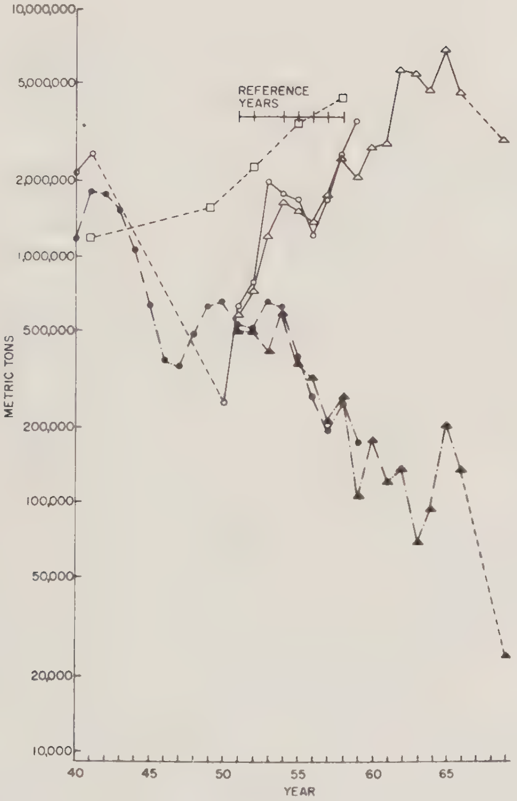


Figure 1.1. A time series comparison of sardine and anchovy biomass estimates from 1940 through 1969. (From Smith, 1972). Dashed lines represent interpolations between non-adjacent years.

● - sardine biomass from 1940 to 1959 calculated from the fishery by Murphy (1966)

▲ - sardine biomass from 1951 to 1969 derived from a regression estimate of the relationship between the Murphy biomass estimate and the sardine larval index (Sections 2.4., 2.5.) determined during the reference years

o - anchovy biomass from 1940 to 1959 derived from the ratio of anchovy larvae to sardine larvae and the Murphy sardine biomass estimate

Δ - anchovy biomass from 1951 to 1969 derived from a regression estimate of the relationship between the anchovy tonnage calculated from the anchovy: sardine larvae ratio, and the anchovy larval index.

□ - Murphy estimate of anchovy spawning biomass by 3-year averages (Murphy, 1966)

Sonic survey is acquiring more and more importance owing to the recent development in acoustic instruments. Although the results obtained to date are not as numerous as those provided by the catch and effort data analysis and tagging experiments, the importance of sonic surveys in the future is expected to be extremely high. This method is used for locating fish schools and even individual fish. However, the interpretation of sonic records requires sampling by fishing operations or other means, such as photography or submersible television to identify the kind of fish. It is difficult to intercept all parts of the stock if fish are moving rapidly either horizontally or vertically unless a number of vessels are used simultaneously for a sonic survey. Methodological limitations of sonic surveys have been considered by Forbes and Nakken (1972).

There are several marked advantages in using fish eggs and larvae to monitor adult populations and estimate biomass. The early life history stages of fishes are restricted, by depth, usually to the upper mixed layers. The passive eggs and feebly swimming larvae are quite vulnerable to capture. Many marine fishes have pelagic eggs and most have pelagic larvae. Thus, it is easy to quantitatively sample several species over broad areas with a simple plankton net. This type of gear can be handled by a wide variety of vessels without major installations of equipment. The increase in cost for adding species to be studied for biomass estimates is much less when eggs and larvae are used than when adults are used. The index of larval abundance obtained from ichthyoplankton surveys has been shown to provide a reliable estimate of biomass, e.g., for sardine and anchovy (Fig. 1.1) and Pacific mackerel (Fig. 1.2).

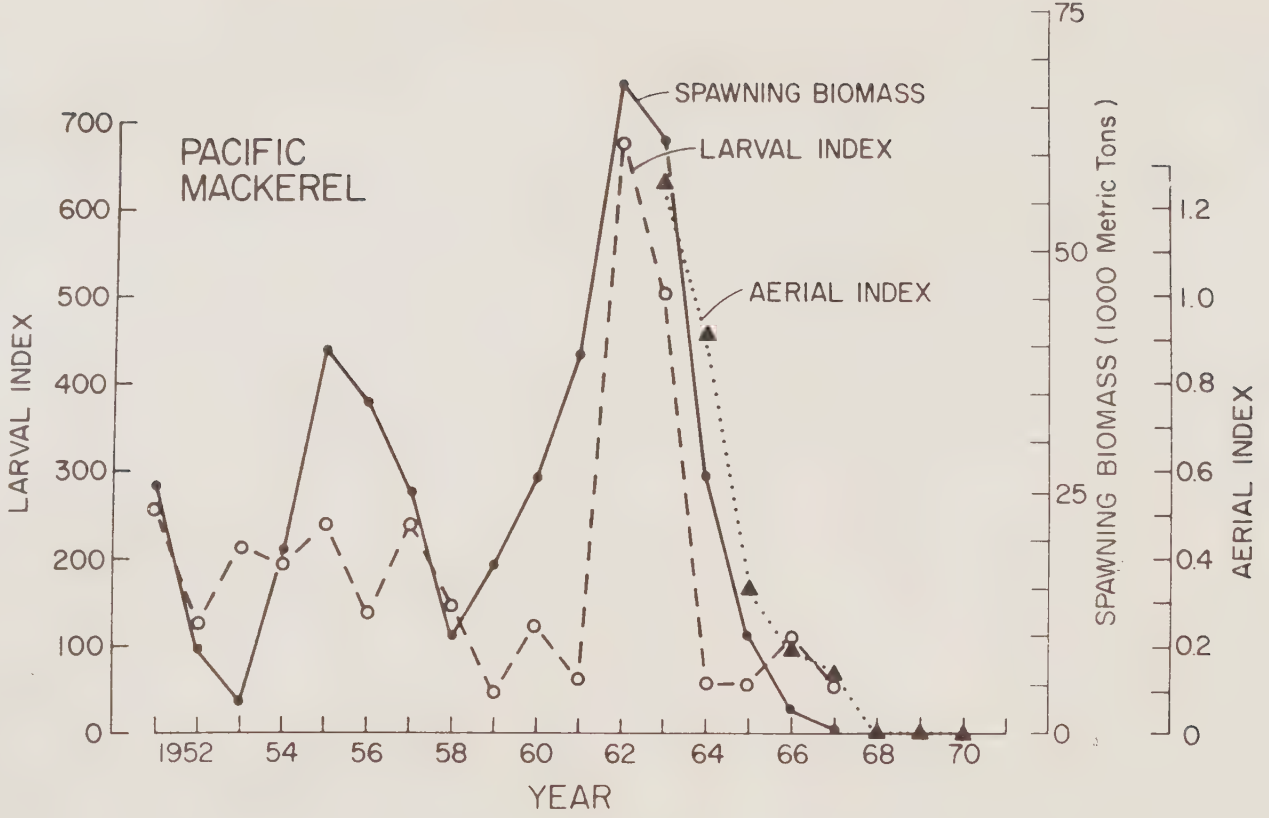


Figure 1.2. Three independent estimates of the stock of Pacific mackerel off Southern California and Baja California, Mexico.

——— estimate of spawning biomass derived by Parrish (1974) from age-specific catch and effort data using methods of Murphy (1966)

----- larval index based on CalCOFI ichthyoplankton surveys (Section 2.4.)

..... aerial index based on the number of schools logged from the air (Squire, 1972).

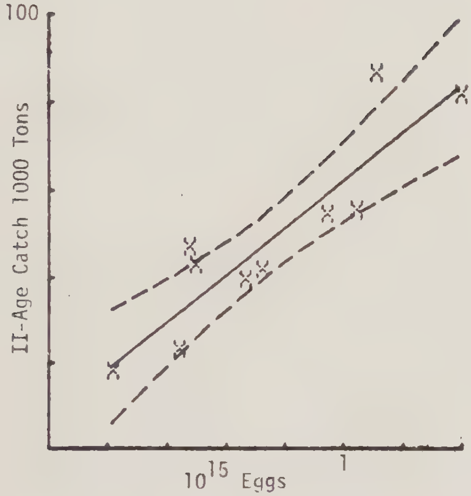


Figure 1.3. Correlation between the abundance of eggs and the adult catch of anchovy in the following fishing season in the Pacific waters along Honshu. (r_s=.91, r_d=.88). (Data from Hayashi, 1961).

There are additional benefits to be obtained from ichthyoplankton surveys primarily designed to estimate spawning biomass. The samples contain not only fish eggs and larvae, but also part of their potential zooplanktonic food and predators. Modern oceanographic techniques allow simultaneous measurements of the physical and chemical environment of planktonic communities. Trends of water motion can be estimated. The survey can detect spatial and temporal isolation efficiently over wide oceanic areas and thereby help define unit stocks of fish upon which fishery management normally depends (Gulland, 1969). Spawning distributions delimited by surveys tell when and where the fish will be concentrated for efficient capture. Results from the survey can be used for monitoring changes in the species composition and diversity of the communities in which the fish stocks reside. Data obtained can be used for forecasting the stock size into the next fishing season (Fig. 1.3.) and for forecasting the year class strength of a species. Ichthyoplankton surveys can also contribute information on new stocks of fish with commercial potential (Ahlstrom, 1968, Gulland, 1970).

Problems associated with the use of ichthyoplankton surveys to estimate spawning biomass are of a taxonomic, technical, and statistical nature. Problems involved with identification stem from the fact that early life history stages have been described in the literature for relatively few of the species. Also, there are a limited number of specialists who are broadly knowledgeable in the identification of fish eggs and larvae. These problems are surmountable (Sections 2.2., 4.). Technical problems involved with the survey require an adequate staff be assembled to handle the collection and processing of samples which may be extensive. Also, high standards must be maintained during the sampling process for quantification and comparison of data (Sections 2.1.2., 3.2.). The statistical problems are inherent in the oceanic sampling process and require the ability to interpret difficult distributions of sample data (Section 3.1.).

1.2. Scope

This manual describes recommended standard procedures for conducting quantitative ichthyoplankton surveys for spawning biomass estimates. This description (Section 2.) covers survey planning and field operations, laboratory procedures, data summarization, making census estimates, and estimating the spawning biomass. Theoretical considerations of the problems and biases involved with the recommended procedures are discussed in Section 3.

A large selected bibliography on ichthyoplankton surveys (FAO Fisheries Circular 706) is being prepared to complement this manual. In addition to papers on survey methods and results, the bibliography includes references on species identification, which is outside the scope of this manual, and tables of cross references of the papers on survey results and species identification by geographic area and taxonomic group. In cases where there are no published works and fish must be reared for identification purposes, the bibliography of May (1971) should be consulted for references on appropriate culture techniques.

2. Recommended Procedures for Conducting Ichthyoplankton Surveys for Spawning Biomass Estimates

The chief barriers to the successful execution of surveys and delivery of survey results are 1) underestimation of the necessary technical effort, and 2) imprecise definition of survey objectives. Most new ichthyoplankton surveys will encounter a mixture of new problems, specific to the survey area, and problems which have been well-defined and solved in older surveys. This section of the manual will be directed toward the standard methods recommended on the basis of survey experience so that the newer surveys may best encounter and solve the problems specific to the new survey environment.

The planning stage is likely to be the most important part of the survey for this is where the objectives of the survey are compared with monetary and personnel resources. The commitment of money and time to the surveys is an irreversible step. To minimize risk, it is necessary to set phased re-evaluations of objectives and survey performance. This process should be incorporated into the planning so that the tactics of the survey may evolve toward the most effective delivery of survey results.

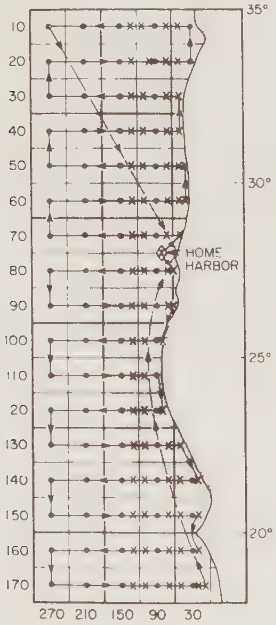


Figure 2.1. An example of a centric systematic area sample grid (Milne, 1959) superimposed on a hypothetical coastal spawning area. The solid dots represent complete biological oceanographic sampling stations and the "X's" represent supplementary stations for detailing coastal gradients. The lines connecting the stations represent a possible method of occupying each station with two ships. The diamond-enclosed "X" represents a test station occupied by both ships on each cruise to check the completeness and operability of the ship's survey equipment and to compare the performance of each ship's measuring equipment.

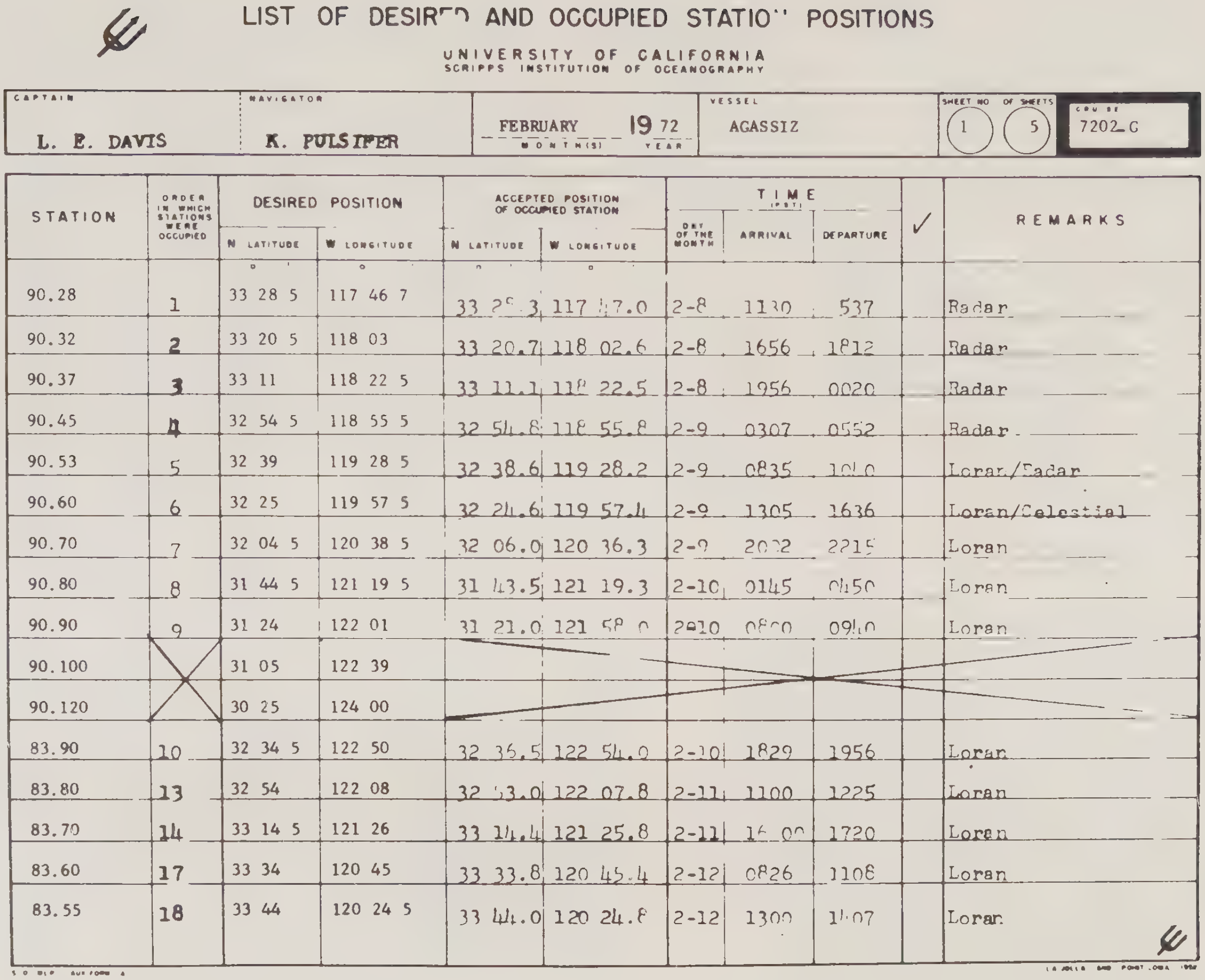
2.1. Field Operations

In this example, it is considered that the field operations will be conducted from ships 15 to 100 meters in length which are equipped to make plankton tows and hydrographic observations.

2.1.1. Cruise Plan and Personnel

Normally the cruise plan (Section 3.3.) is prepared by the chief scientist and the chief marine technician. After the cruise track is prepared, it is discussed with the ship's captain. Figure 2.1 shows a two-ship cruise plan to measure the extent and intensity of spawning in the outlined area.

Log sheets ("Captain's sheets") which list the desired stations and their positions, the order in which the stations are to be occupied, the captain and the navigator for the cruise ship, the month and year of the cruise, and the name of the ship (Fig. 2.2) are filled out by the chief scientist and the chief marine technician before each cruise. During the cruise, information is added to these sheets including station position actually occupied, the day of the month, the time of arrival to and departure from the station, and the method for locating the station position. Omitted stations are noted and the order in which the stations were actually occupied is corrected accordingly.



LIST OF DESIR⁻ᴰ AND OCCUPIED STATIO·· POSITIONS

UNIVERSITY OF CALIFORNIA
SCRIPPS INSTITUTION OF OCEANOGRAPHY

CAPTAIN L. E. DAVIS	NAVIGATOR K. PULSIFER	FEBRUARY 19 72 MONTH(S) YEAR	VESSEL AGASSIZ	SHEET NO 1	OF SHEETS 5	CRUISE 7202_C

STATION	ORDER IN WHICH STATIONS WERE OCCUPIED	DESIRED POSITION N LATITUDE ° '	DESIRED POSITION W LONGITUDE ° '	ACCEPTED POSITION OF OCCUPIED STATION N LATITUDE ° '	ACCEPTED POSITION OF OCCUPIED STATION W LONGITUDE ° '	TIME (PST) DAY OF THE MONTH	TIME (PST) ARRIVAL	TIME (PST) DEPARTURE	✓	REMARKS
90.28	1	33 28 5	117 46 7	33 28.3	117 47.0	2-8	1130	537		Radar
90.32	2	33 20 5	118 03	33 20.7	118 02.6	2-8	1656	1812		Radar
90.37	3	33 11	118 22 5	33 11.1	118 22.5	2-8	1956	0020		Radar
90.45	4	32 54 5	118 55 5	32 54.8	118 55.8	2-9	0307	0552		Radar
90.53	5	32 39	119 28 5	32 38.6	119 28.2	2-9	0835	1040		Loran/Radar
90.60	6	32 25	119 57 5	32 24.6	119 57.4	2-9	1305	1636		Loran/Celestial
90.70	7	32 04 5	120 38 5	32 06.0	120 36.3	2-9	2032	2215		Loran
90.80	8	31 44 5	121 19 5	31 43.5	121 19.3	2-10	0145	0450		Loran
90.90	9	31 24	122 01	31 21.0	121 58.0	2-10	0800	0940		Loran
90.100		31 05	122 39							
90.120		30 25	124 00							
83.90	10	32 34 5	122 50	32 35.5	122 54.0	2-10	1829	1956		Loran
83.80	13	32 54	122 08	32 53.0	122 07.8	2-11	1100	1225		Loran
83.70	14	33 14 5	121 26	33 14.4	121 25.8	2-11	1600	1720		Loran
83.60	17	33 34	120 45	33 33.8	120 45.4	2-12	0826	1108		Loran
83.55	18	33 44	120 24 5	33 44.0	120 24.8	2-12	1300	1407		Loran

Figure 2.2. List of desired and occupied station positions, the "Captain's sheets". (Courtesy University of California, Scripps Institution of Oceanography.)

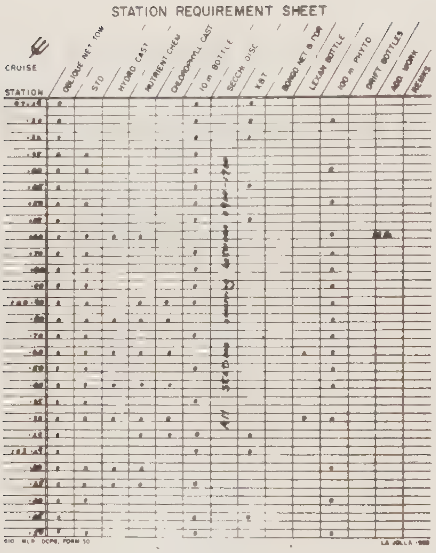

STATION REQUIREMENT SHEET
CRUISE
STATION
OBLIQUE NET TOW
STD
HYDRO CAST
NUTRIENT CHEM
CHLOROPHYLL CAST
10 m BOTTLE
SECCHI DISC
XBT
BONGO NET & TOW
LEXAN BOTTLE
100 m PHYTO
DRIFT BOTTLES
ADD WORK
REMARKS
SIO WLR DCPG FORM 10
LA JOLLA 1966

Figure 2.3. Station requirement sheet. (Courtesy University of California, Scripps Institution of Oceanography.)

The chief scientist and the chief marine technician also fill out a station requirement sheet, (Fig. 2.3.) which lists the stations the same as the "Captain's sheets" but includes additional information of the number and type of observations to be carried out on each station. Copies on this sheet are provided to each cruise leader (one of whom may be the chief marine technician). Following the description of the cruise on the station requirement sheet, the chief marine technician and the cruise leader select the marine technicians and watch leaders required for each cruise. Following the selection of the scientific staff for the cruise, a cruise announcement is issued which provides the beginning date and the proposed final date of the cruise, the objectives and procedures for the cruise and the personnel who are to conduct the cruise.

It must be stressed that having an experienced, responsible marine technician (who may also serve as cruise leader) is essential to the success of the survey. Duties assigned to the chief marine technician go far beyond those involved with setting up the cruise plan. He is responsible for seeing that the station procedures (Sections 2.1.2., 2.1.3., and 2.1.4) are carried out correctly for each station that is occupied.

2.1.2. Sampling System

The recommended sampling system requires that the ship be equipped with a hydrographic winch with more than 400 meters of standard hydrographic wire (i.e., 0.48 cm in diameter), a meter block or a metering system on the winch to measure the amount of wire out and an angle indicator (inclinometer) to measure the angle at which the wire enters the water.

2.1.2.1. The Sampler

The Bongo net (Figs. 2.4 and 2.5) towed at slow speeds, is recommended as the best type of simple gear fished from hydrographic winches for ichthyoplankton surveys. It provides a minimum of variation in the biases caused by uneven filtration per unit depth, avoidance of the net, and escapement or extrusion of organisms through the meshes. This recommended "slow" Bongo equipment is derived from bridle-free plankton nets (McGowan and Brown, 1966). It incorporates simplifications from the original opening-closing design suggested by Posgay, Marak, and Hennemuth (1968) as well as modifications made by Smith, Thrailkill, and Vrooman (1971)* after extensive comparison of the Bongo net and the CalCOFI standard net (Vrooman, 1972).**

The Bongo towing frame (Fig. 2.4) made of anodized aluminum, consists of two circular frames, each 0.6 m in diameter, connected by a central yoke to which the towing

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* Cruise Report. David Starr Jordan #59. Dated April 1971. On file at Southwest Fisheries Center, La Jolla, California.

** Cruise Report. David Starr Jordan #70. Dated June 1972. On file at Southwest Fisheries Center, La Jolla, California.

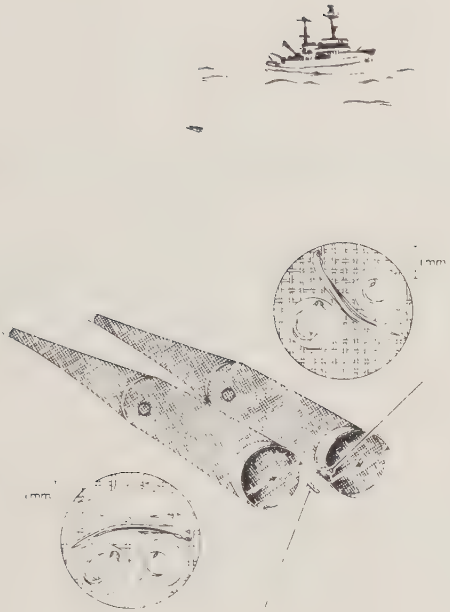


Figure 2.4. The Bongo net recommended for ichthyoplankton sampling.

wire is attached. Thus there are no bridles in front of the mouth of the net. A 22 kilogram dead weight depressor is suspended beneath the frame (Fig. 2.5) for making standard oblique tows.

The towing frame is fitted with two cylindrical-conical nets (Figs. 2.4, and 2.5) made of Nitex or equivalent monofilament netting preferably of a dark color. One net, which is the principal ichthyoplankton sample net, has a 0.505 mm mesh. The other net, which may be used for plankton biomass studies or fish egg and larva escapement and extrusion studies (Lenarz, 1972), should have a 0.333 mm mesh. The use of "soft" cod ends (Fig. 2.6) is recommended primarily as a matter of handling ease. Sample spillage back into the net is less likely to occur than with a "hard" cod end. The cod ends are made of the same type netting and mesh size as the main part of the net. The nets and the cod ends are color-coded for easy recognition and match up of mesh size (e.g., red for the .505 mm mesh and blue for the .333 mm mesh).

A flowmeter is mounted in the mouth of each net (Fig. 2.5) to provide data on the volume of water filtered during each tow. This information is essential for quantification of the data.

2.1.2.2. The Towing Procedure and Data Records

The standard towing procedure is modified from Kramer *et al*. (1972). An example of an on-deck arrangement for making plankton tows is provided in Fig. 2.7.

The data sheet - Before the station is occupied, the following numbered items are recorded on the plankton-tow data sheet, a sample of which is in Fig. 2.8. (The data sheets are made of a water resistant linen which will not deteriorate when handled or when wet.)

Item 1	Cruise
Item 3	Date
Item 4	Order occupied
Item 5	Station
Item 11	Net number (= mesh size) for regular and fine mesh.
Item 12	Meter number (= flowmeter number) for regular and fine mesh.

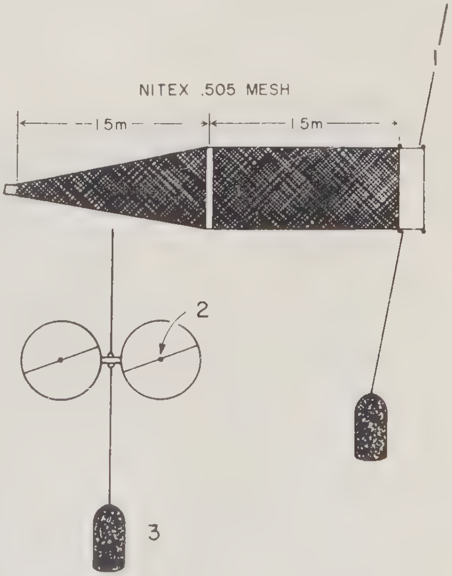


Figure 2.5. Diagrammatic view of the recommended Bongo net: 1) 0.48 cm (3/16 in.) cable from meter block on research vessel, 2) flowmeter suspended within the mouth of each net, 3) 22 kg. (50 lb.) hydrographic weight.

Item 14. Initial flowmeter reading (carryover from last tow) for regular and fine mesh.

Additional data to be recorded during the tow are mentioned as the towing procedure is described.

The tow - After the gear is assembled and the data sheet for the plankton tow is prepared (as outlined above), the tow is ready to begin. The net tow is made off either side of the ship as follows: (Tows off the stern are not recommended because of turbulence from the ship's propeller.)

1. The ship is stopped on station. Bottom depth on station is requested from the bridge and recorded in the lower left-hand section of the data sheet. Note: The bottom depth will determine the depth to which the nets will be lowered and thus the length of wire to be let out. To lower the net to 210m (the standard procedure for this type of survey, depth permitting) with a wire angle of 45° requires that 300m of wire be let out (wire angle is defined as deviation from the vertical) :

$$\text{Length of wire out X cosine } 45° = \text{net depth}$$

$$300\text{m X } 0.707 = 210\text{m}$$

If station depth is less than 238m, reference to the "depth of tow" graph (Fig. 2.9) will quickly give the proper amount of wire to be let out so that the net will not hit the bottom. For shallow tows, the wire is let out and retrieved at the same rate as for routine standard tows to avoid relative over-sampling of the surface layers. The standard tow filters 1 to 2 cubic meters of water for each meter depth. Alteration in the rate at which the wire is let out or retrieved would materially affect the basic statistical distribution of sample size.

2. The flowmeter is read and checked against the recorded initial meter reading (Item 14 on the tow data sheet). If there had been a previous tow, this should have been the final meter reading (Item 13 on the previous tow data sheet). If the reading changed between tows, the last recording is crossed out, the new reading is

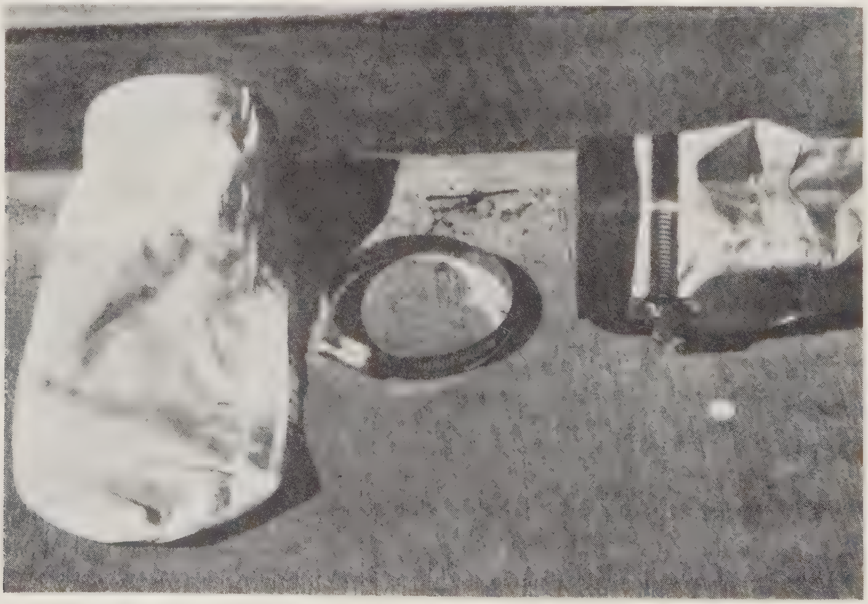


Figure 2.6. "Soft" cod end made of Nytex. (From Kramer *et al.*, 1972)

entered, and an explanation is given in the lower right-hand part of the data sheet under "Remarks".

3. The 22 kg weight is lowered below the surface of the water. If the ship is still slightly underway, the wire (#6 in Fig. 2.7) is pulled to the side of the work-platform (#10 in Fig. 2.7) and fastened close with a snap hook attached to the outside rail.

4 The inclinometer is fastened to the wire above the Bongo net (Fig. 2.7). Enough slack is left on the line to the inclinometer so that when the proper angle is achieved during the tow, it will not ride up on the cable to hit the block. (If the survey is for net tows only, the inclinometer may be left on the tow wire.)

5. The winch meter is zeroed. The ship is set underway, wind off the bow on the side on which the tow is taken, and the signal to start the tow is given from the bridge. The blocks or pins, which keep the blades of the flowmeters from revolving between tows are removed, and the Bongo net is lowered into the water. (Some flowmeters have "automatic" blocks that release the impeller blades when water flows through them.)

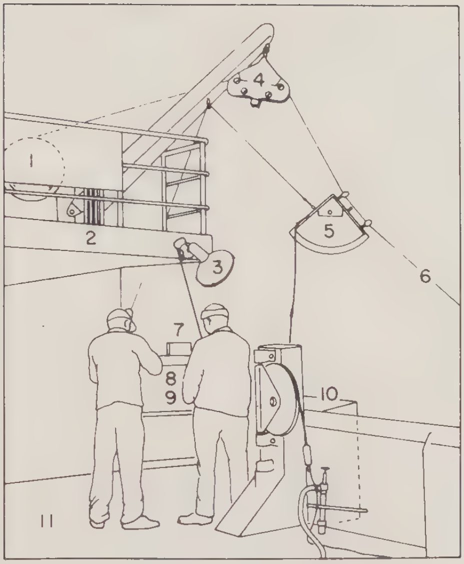


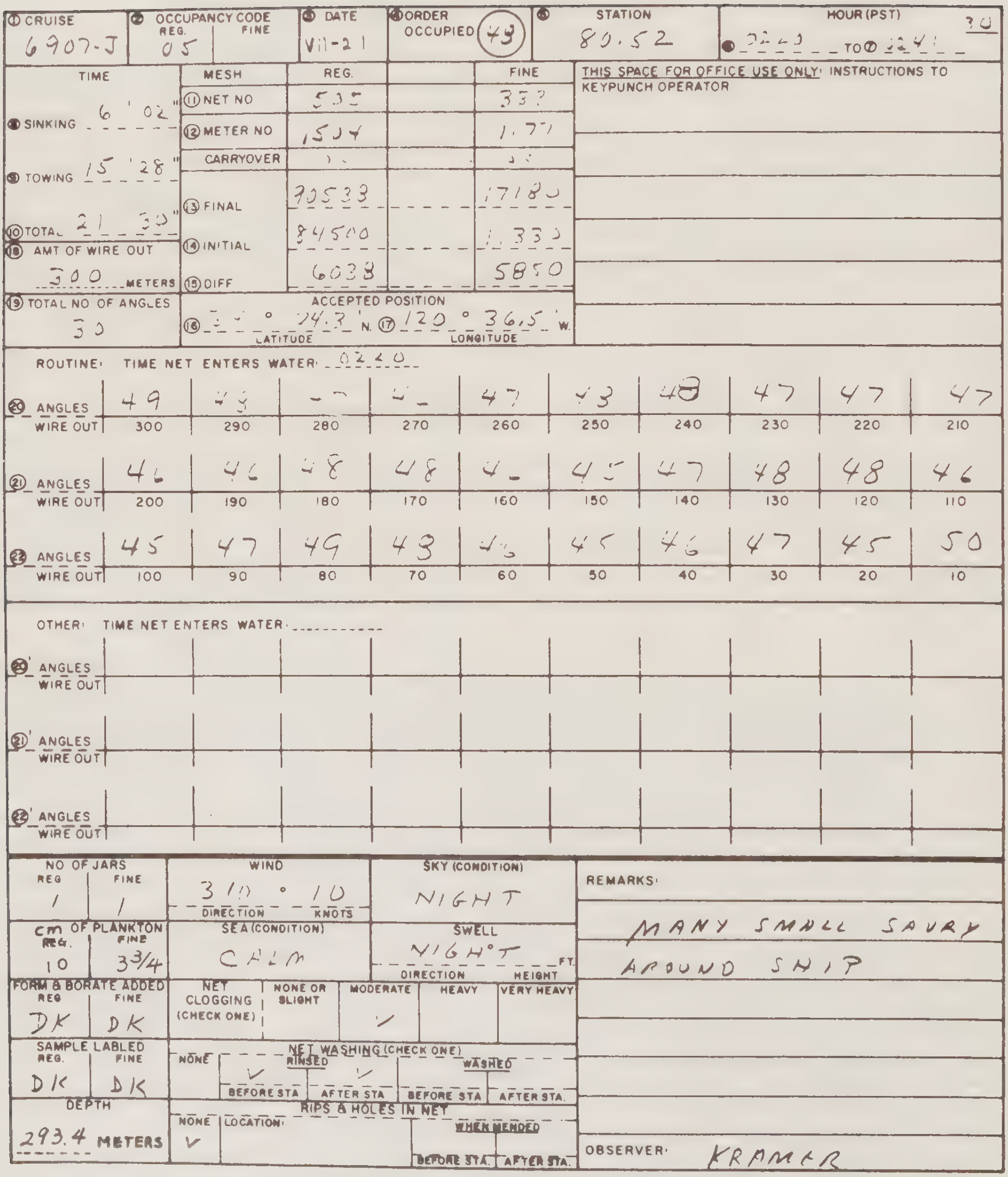
Figure 2.7. The on-deck layout of the ichthyoplankton towing apparatus on the U.S. National Marine Fisheries Service research vessel David Starr Jordan. 1) Winch drum which holds the hydrographic wire. 2) Boat deck. 3) Flood lamp for illuminating immediate area of inclinometer and overside platform. 4) Meter block which is connected to readouts in ship's bridge, dry laboratory and, and winch console and gives an instantaneous reading of meters of wire out. 5) Inclinometer which indicates angle of stray of towing wire. 6) Towing wire which is 0.48cm (3/16 in.) in diameter. 7) Intercommunications device which allows communication between bridge and winch operator during tow. 8) Meter block readout on winch console. 9) Winch and boom controls at winch console. 10) Overside work platform for hooking up inclinometer and, launching and retrieving Bongo net. (Adapted and modified from Kramer *et al*., 1972)

a. The nets are allowed to stream out briefly before lowering. As soon as it is obvious that they are not tangled, the wire is immediately let out the predetermined amount at a constant rate of 50 m/min.

b. The stopwatch is started as soon as the flowmeters are seen to sink below the surface of the water. The stopwatch is used to record sinking time (Item 8) and towing time (Item 9) in seconds. The duration of the tow in seconds is used for calculation of mean velocity of towing.

c. The time the net enters the water is recorded in nautical time (2400 hr) to the nearest 5 min. (Item 6, and Item 20 or 20' depending on whether the tow is "Routine" or "Other"). The time of day is used for analysis and correction of day-night differences in the catching power of the net.

d. When the desired amount of wire has been let out, the stopwatch is stopped, the sinking time is recorded in seconds (Item 8), the



① CRUISE 6907-J	② OCCUPANCY CODE REG. 05 FINE	③ DATE VII-21	④ ORDER OCCUPIED 43	⑤ STATION 80.52	HOUR (PST) 30 ⑥ 0220 TO ⑦ 0241

TIME	MESH	REG.		FINE
⑧ SINKING 6 ' 02 "	⑪ NET NO	535		337
⑨ TOWING 15 ' 28 "	⑫ METER NO	1504		1077
	CARRYOVER	[illegible]		[illegible]
⑩ TOTAL 21 ' 30 "	⑬ FINAL	90533		17180
⑱ AMT OF WIRE OUT	⑭ INITIAL	84500		11330
300 METERS	⑮ DIFF	6038		5850

THIS SPACE FOR OFFICE USE ONLY: INSTRUCTIONS TO KEYPUNCH OPERATOR

⑲ TOTAL NO OF ANGLES 30

ACCEPTED POSITION ⑯ [illegible] ° 24.3 ' N. ⑰ 120 ° 36.5 ' W.
LATITUDE LONGITUDE

ROUTINE: TIME NET ENTERS WATER: 0220

⑳ ANGLES	49	43	[illegible]	[illegible]	47	43	48	47	47	47
WIRE OUT	300	290	280	270	260	250	240	230	220	210
㉑ ANGLES	46	46	48	48	[illegible]	45	47	48	48	46
WIRE OUT	200	190	180	170	160	150	140	130	120	110
㉒ ANGLES	45	47	49	43	46	45	46	47	45	50
WIRE OUT	100	90	80	70	60	50	40	30	20	10

OTHER: TIME NET ENTERS WATER:

⑳' ANGLES										
WIRE OUT										
㉑' ANGLES										
WIRE OUT										
㉒' ANGLES										
WIRE OUT										

NO OF JARS REG 1 FINE 1	WIND 310 ° 10 DIRECTION KNOTS	SKY (CONDITION) NIGHT
cm OF PLANKTON REG. 10 FINE 3¾	SEA (CONDITION) CALM	SWELL NIGHT FT. DIRECTION HEIGHT

FORM & BORATE ADDED	NET CLOGGING (CHECK ONE)	NONE OR SLIGHT	MODERATE	HEAVY	VERY HEAVY
REG DK FINE DK			✓		

SAMPLE LABLED	NET WASHING (CHECK ONE)				
	NONE	RINSED		WASHED	
		BEFORE STA	AFTER STA	BEFORE STA	AFTER STA.
REG. DK FINE DK		✓	✓		

DEPTH	RIPS & HOLES IN NET		WHEN MENDED	
	NONE	LOCATION:	BEFORE STA.	AFTER STA.
293.4 METERS	✓			

REMARKS: MANY SMALL SAURY AROUND SHIP

OBSERVER: KRAMER

Figure 2.8. Plankton tow data sheet. (From Kramer et al., 1972). A sample copy of a sheet made out for station 80.52 on cruise 6907-J.

stopwatch is zeroed and restarted immediately. (Since the net is "fishing" on the way down, sinking time is as important as that of retrieval.)

e. When the stopwatch is restarted, the nets are left at the desired depth for 30 sec. (hypothesizing that "falling" nets will straighten out at depth in the 30-sec. interval).

f. At the end of 30 sec. the stopwatch is not stopped, the wire angle is recorded for that depth, and retrieval is begun at the rate of 10 m per 30 sec. for all tows. The wire angle is recorded at every 10 m (Item 20 to 22 for routine tows with 300 m of wire out or Items 20' to 22' for other tows). Note: Ship speed, during sinking, during times at depth, and during retrieval, is maintained to keep the wire angle at 45°. In dead calm, it may be necessary to run the ship in circles to maintain the wire angle. It is essential to maintain the 45° ($\pm 3°$) wire angle to assure that the proper amount of water is being filtered from each depth (1 to 2 cubic meters per each meter depth) for purposes of data quantification.

g. The nets are brought directly out of the water at a steady rate. Note: It is important not to allow the nets to fish too long at the surface because of the bias that results from oversampling surface waters (Section 3.2.1.). When the flowmeters break the water surface, the stopwatch is stopped and its reading in seconds is recorded as the towing time (Item 9). Note: If the flowmeters are the kind that do not have "automatic" blocks on the impeller blades, blocks or pins should be placed in them to stop the impeller blades from rotating as soon as possible after the flowmeters break the water surface.

6. The nets are washed down from the outside to get all the plankton into the cod ends, keeping the net rings at rail height with the cod ends dangling. A salt water hose is used for the washing. Water pressure should be enough to loosen the plankton adhering to the net mesh but not so much as to damage the plankton organisms. This operation usually takes only a few minutes per net.

7. After all the plankton has been washed into the cod ends, the nets are brought aboard. The color-coded cod ends (e.g., red for .505 mm mesh and blue for 0.333 mm mesh) are removed, keeping the plankton from spilling back into the nets. The plankton samples are taken to the ship's wet laboratory and preserved immediately (Section 2.1.3.1.).

8. After the samples have been preserved, labelled, and stored, the cod ends are washed (they may be left everted) and replaced on the nets with matching color codes in preaparation for the next tow.

9. Before leaving the station, the flowmeters are read and recorded as the final readings (Item 13). The initial readings (Item 14), which were made before the tow began, are subtracted from the final readings (Item 13) to get the differences (Item 15) which are the number of revolutions for the tow for each net. Note: It is important that the proper amount of water has been filtered for quality of tow and data quantification. For each flowmeter, the proposed central number of revolutions and acceptable limits to this number of revolutions should be calculated before the cruise to serve as a guide for the observer to tell if the tow has been correctly conducted. If meter readings are not normal, the net tow may have to be repeated. A very high reading may have been caused by too great a ship's speed - check for many high wire angles. A low reading may have been due to too slow a ship's speed - check for many low wire angles. Another reason for low meter readings may be clogging of the nets. This may be cumulative if a net is not rinsed properly or it may occur at a single station. If a meter shows a trend toward lower and lower readings, and it is not malfunctioning, the net should be washed (Section 2.1.2.2., #15). The net tow need not be repeated if it is obvious that heavy clogging is the reason for low readings (it will only clog again) or if the ship's speed has caused low or high angles. If wire angles are normal, the net is clean, and the towing time (Section 2.1.2.2. #11) is routine but the meter reading is low, the cause could be that a bit of detritus, a fish, or even a large jelly or salp had become entangled in the meter blades for a portion of the tow. Under these conditions, the tow should be repeated. If the

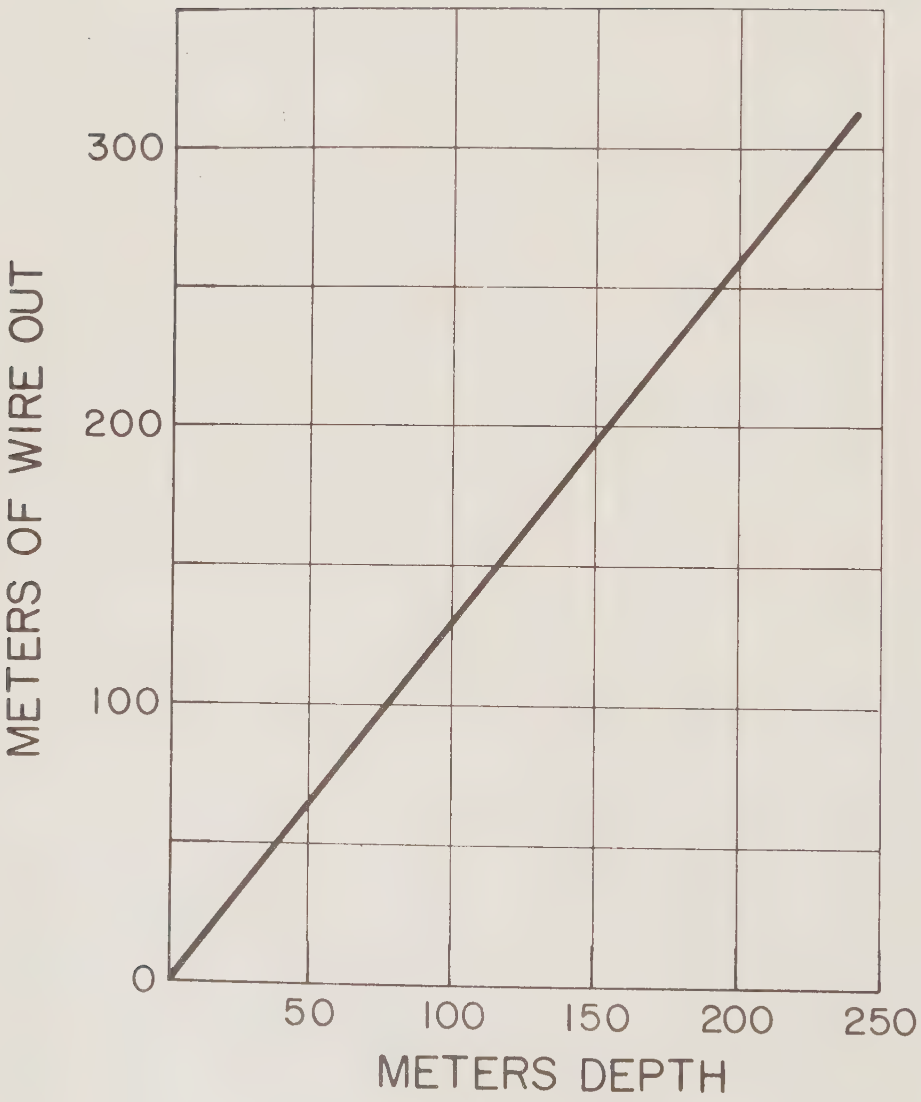


Figure 2.9. Depth-of-tow graph. (Modified from Kramer *et al.*, 1972).

reading is again very low and it is obvious that the flowmeter is not functioning properly, replace the meter and repeat the tow. Do not oil or grease any meter or make any repairs that might alter the rotation of the blades. Repairs of this type would seriously affect the calibration of the meter. If clogging is apparent, the amount is recorded in the appropriate box on the plankton tow data sheet.

10. Wind, sky, sea condition and sea swell should be requested from a crew member by the observer who is recording the angles while the tow is being made. The information is recorded in the appropriate boxes in the lower section of the plankton tow data sheet.

11. Total towing time (Item 16) is recorded as the sum of Items 8 and 9. For a 300 m tow, total time should be about 21'30" (6' sinking time + 15'30" towing time). Note: If total time is off by 15 to 20 sec., it must be explained in the "Remarks" section. The most usual variation will be in the sinking time, caused by a slightly faster or slower rate in paying out the wire than the recommended 50 m/min. In certain conditions, such as poor control of the ship, countercurrents below the sea surface adversely controlling the net as it falls, etc., the winch operator may have to depart from the sinking-time procedures to slow the falling net in order to keep it from becoming tangled. Such departures from normal procedures must be recorded in the "Remarks" section.

12. Total towing time is added, in minutes and seconds to Item 6 to record the hour, minutes and seconds in Item 7. This is actually the time the net comes out of the water.

13. The actual station position (accepted position) is recorded in Items 16 and 17. This may be done when the station is occupied, but usually is done at the end of the cruise when the captain has compiled a complete list of the positions of all stations (Section 2.1.1.).

14. Checks are made regarding the sample (Section 2.1.3.) and appropriately recorded on the tow data sheet in the lower left-hand section.

a. Number of jars per sample.

b. Centimeters of plankton - this gives approximate volume before water is added.

c. Formalin and sodium borate added - the person who adds the preservative and buffer must initial this box for each sample after the Formalin and sodium borate are added.

d. Sample labelled - the person who labels the sample must initial this box after the sample is labelled.

15. Checks are made on the net to see if washing or repair is necessary. The appropriate boxes are checked in the lower section of the tow data sheet. If replacement of a net is necessary, it should be recorded in the "Remarks" section.

a. If washing is needed, one of three methods may be used: (1) The net is everted, still on its ring, and brushed down with an ordinary sweeping broom and running sea water; (2) The rings are stood on edge, the net is tightened along its length by tying down the end (without cod end attached) and hosed down with a high-pressure fire hose. This is very effective provided that plankton has not dried in the meshes; (3) The net is detached from the ring and put in a washing machine using a 30-min. cycle, war water (not hot) and a non-polluting detergent.

b. Rips and holes in the net - the net should be examined after every tow to check on needs for repair or replacement. If holes or tears are small, they should be sewn before the next tow with nylon thread of a color (e.g., red) that can be easily located for sewing machine repair later on shore. If the net is torn beyond mending at sea, replace the net.

16. Recheck the tow data sheet to be sure that all items are filled in. (The occupancy code, Item 2, is filled in onshore at the end of the cruise. This is usually one of a series of numbers used by a computer programmer to describe the type of tow or the station occupied.) Note: Some deviations from standard procedure cannot be avoided. Circumstances such as strong under-sea currents, high winds, heavy seas, will cause unavoidable deviations, e.g., odd meter readings, prolonged stops at stations. Conditions of this kind should be noted in the "Remarks" section.

17. A new plankton tow data sheet is set up for the next station: Items 1, 3, 4, 5, 11, 12, and 14 are entered. Item 14 should be the final reading of the preceding tow and should be rechecked before starting next tow.

2.1.3. Handling the Sample at Sea

Fish eggs and larvae are fragile and easily damaged. Proper care is needed in all stages of preservation and handling plankton samples aboard ship.

2.1.3.1. Preserving the Sample

The plankton sample should be preserved immediately. This is especially critical in tropical waters.

The storage container in which the sample is preserved should be of sufficient size so that when filled, the preserving liquid (5% buffered Formalin is recommended) will occupy at least three times the volume of the plankton. No problems are posed in having a large ratio of preserving liquid to plankton. Glass jars holding 1000 ml are recommended. Normally they are closed by a screwed-on plastic lid with an inside coating to prevent leakage and evaporation.

The plankton collection is carefully poured from the cod end into the container in which it will be stored. The cod end is then rinsed down to gather the last of the plankton at its bottom. When fairly well drained, the cod end is everted over and into the jar and the remaining plankton is washed off carefully. It has to be ensured that no parts of the sample remain on the mesh of the cod end.

At this point, before seawater is added, the height of the plankton in the jar is measured in centimeters. This gives an approximate volume to be recorded on the plankton tow data sheet (Section 2.1.2.2., #14).

The jar containing the plankton is then filled three-fourths full with seawater before adding the preservative (full strength Formalin) and buffer (sodium borate). This is done to avoid "burning" the delicate plankton organisms. To obtain the recommended 5% solution of Formalin in a one-liter jar, 50 ml of concentrated commercial Formalin is added. To assure proper buffering, 20 ml of a saturated

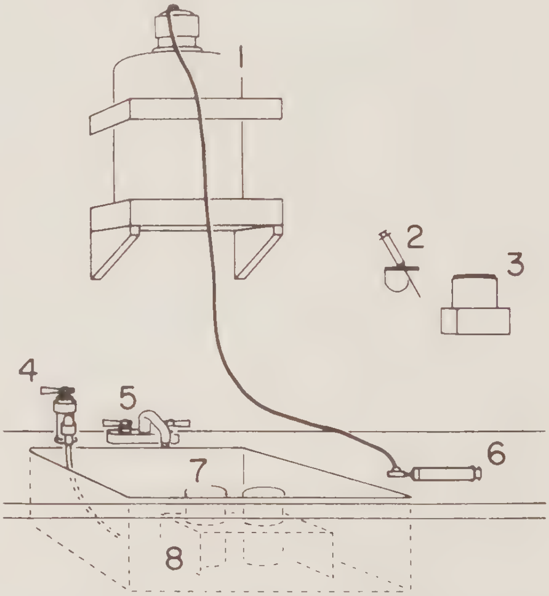
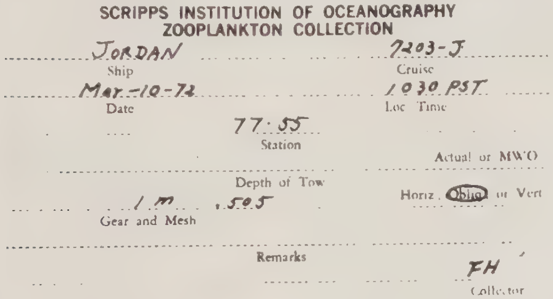


Figure 2.10. Ship's wet laboratory setup for preserving and labelling plankton samples. 1) Plastic carboy (19 liters) containing concentrated formaldehyde and having 1.5 m of surgical tubing. 2) 20 ml disposable syringe with cannula for adding buffer to plankton samples. 3) Container of sodium borate in seawater. 4) Salt water tap with 0.5 m of surgical tubing to rinse cod end, concentrate plankton, and fill sample jar after fixation and buffering. 5) Ship's hot and cold freshwater taps. 6) 50 ml disposable syringe with automatic double valve for measuring and dispensing formaldehyde. 7) 1 liter sample jars. 8) Removable wooden frame to support sample jars in rough weather. The entire assembly, including sink, can be fitted into 1 to 2 m^2 of laboratory bench space. (Adapted and modified from Kramer et al., 1972.)

solution of sodium borate in seawater is added for each liter of preserved sample. (Buffer is added to counteract the acidity of plankton in Formalin. Hexamine should definitely not be used as a buffer. A solution containing too much or too strong a buffer is harmful to fish larvae.) The sample jar is then filled almost to the top with seawater, capped and shaken lightly (including inversion) to obtain immediate, uniform preservation of the plankton organisms throughout the sample.

Data on the number of jars per sample and addition of Formalin and borate to the sample must be entered on the plankton tow data sheet (Section 2.1.2.2., #14). Note: full strength formaldehyde aboard ship is kept in 19 liter polypropylene carboys (Fig. 2.10). With the carboy moored securely above the sink, the preservative is drawn by siphon action. A further safety measure is to draw the formaldehyde via a teflon tube into a 50-ml plastic syringe through an automatic double valve. The buffer is added with a 20-ml plastic syringe fitted with cannula (a "needle" without a point).

Formalin is the most widely used preservative for plankton collections. It is by no means "ideal", but satisfactory when properly handled. Years of experience have shown that too strong or too weak a concentration of Formalin can be damaging to ichthyoplankton. The recommended concentration of 5% for preserving the sample and 3% for later storage of eggs and larvae (Section 2.2.3.) have proven to work well over a long time scale. Other recommendations have been recently proposed (Steedman, 1976; UNESCO, 1974).



SCRIPPS INSTITUTION OF OCEANOGRAPHY
ZOOPLANKTON COLLECTION

Ship: JORDAN
Cruise: 7203-J
Date: Mar-10-72
Loc Time: 1030 PST
Station: 77:55
Actual or MWO:
Depth of Tow:
Horiz, [✓ Obliq] or Vert
Gear and Mesh: 1 m .505
Remarks:
Collector: FH

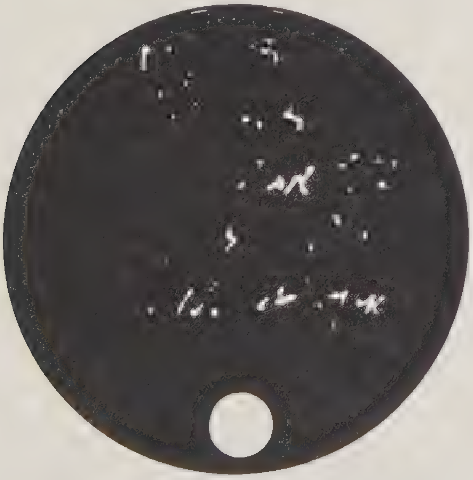


Figure 2.11. Labels for field identification of plankton samples. A. Inside paper label (Courtesy University of California, Scripps Institution of Oceanography). B. Outside label on jar lid.

The concentrated, commercial preparation of Formalin is a 40 percent solution of formaldehyde gas in water. Formalin should be stored in inert containers, glass or plastic, not in metal containers; Formalin reacts with the latter. One of the problems in storage of concentrated Formalin is its tendency to polymerize - to form para-formaldehyde, a flocculent, white solid.

It should always be kept in mind that formaldehyde is a poison that can irritate skin and cause serious cases of dermatitis. Rubber gloves should be worn when preparing formaldehyde solution, or when handling specimens preserved in Formalin. Formaldehyde fumes can also be irritating to the lungs.

2.1.3.2. Labelling

It is essential that samples be properly labelled. Information contained on the labels should be sufficient to identify the sample with certainty. Each sample jar should have two labels. One label is placed inside the jar. Because this label is often difficult to read unless removed, a second label is placed on the lid of the sample jar. Both labels are necessary because jar lids can be mixed up. Should this happen, the inside label usually assures proper identification of the sample.

The inside label (Fig. 2.11) should be made of heavy weight, chemically resistant linen paper which will not fall apart in the Formalin solution. The label is filled out with a soft carbon pencil which will not fade in the Formalin. This label should contain the following information: name of ship, cruise number, date, time, station designation, depth of tow, gear used, mesh size, type of haul, duration of haul, collector's name, number of jars in the sample (1 of 2, 2 of 2 or 1 of 3, 2 of 3, etc.).

The outside label (Fig. 2.11) is written on the lid of each sample jar with a light-colored waterproof marker or wax pencil. It should contain the following information: cruise number, station, date, time, gear, mesh size, number of jars in the sample (1 of 3, 2 of 3, etc.). This outside label should be color-coded to match the net and cod end mesh sizes. This may be done by using an appropriately colored waterproof marker or colored tape (e.g., red for .505 mm mesh and blue for .333 mm mesh).

After the samples are labelled, the person who labels them should initial the appropriate box on the plankton tow data sheet (Section 2.1.2.2., #14).

2.1.3.3. Storage on the Vessel

Sample jars should be completely filled. This is to prevent agitation of plankton in the jars during rough weather, as will happen if they are only partially filled. Even when filled, some movement of the organisms within a jar is inevitable due to vessel motion (rolling, pitching, etc.). Hence, to minimize damage to the delicate organisms during the storage on the vessel, samples should be stored in the most stable part of the ship.

Temperature of storage may be important, particularly in tropical regions. This factor seldom has been given much attention. Collections from tropical expeditions often are of poor quality, even when care has been taken in their preservation and handling. Experiments are needed to test the effect of storage temperatures on the condition of plankton organisms, especially during long cruises. It may be found that air conditioned (temperature-controlled) storage rooms are essential for the proper care of plankton collections on tropical expeditions.

2.1.4. Supplementary Data

At the critical stages in the life history of young fish, minor changes in the environment can cause extensive mortalities and lead to corresponding fluctuations in the abundance and availability of fish stocks. It is therefore important to collect environmental information during the course of ichthyoplankton surveys.

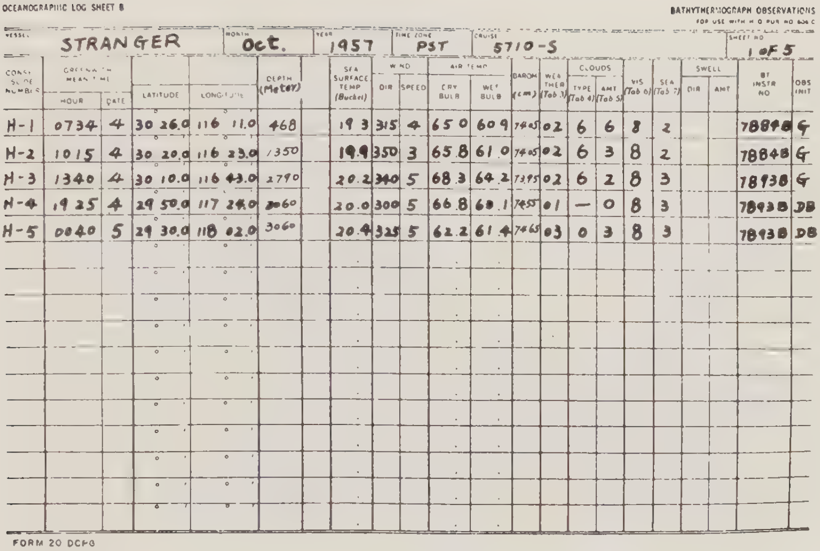
2.1.4.1. Hydrographic Data

For the standard ichthyoplankton survey, it is important to obtain at least some physical oceanographic data at each station. This usually includes a surface temperature taken with a bucket thermometer, and more importantly a bathythermograph (BT) or expendable bathythermograph (XBT) observation to obtain a profile of temperature with depth. A sample data sheet for use with BT observations is in Fig. 2.12. (If an XBT is used, the "BT instrument number" column is left blank).

Additional observations could include samples of water for determination of salinity, oxygen, and nutrients and a Secchi disc reading at day stations.

2.1.4.2. Smaller Zooplankton and Phytoplankton

Information on the availability and utilization of the food of larvae can be obtained by simultaneously sampling for the smaller plankton constituents eaten by the larvae. For studying these organisms, it is recommended that paired Bongo nets, 20 cm in diameter at the mouth, be used. One net should be fitted with netting of 0.250 mm mesh apertures and the other with 0.150 mm mesh. These nets can be fastened to the towing cable immediately above the 60 cm Bongo assembly (Fig. 2.13). It is also highly desirable to measure photosynthetic pigments. The zooplankton in the smaller nets and the photosynthetic pigment data will provide a standard base for comparing the relative productivity of the areas investigated.



OCEANOGRAPHIC LOG SHEET B

BATHYTHERMOGRAPH OBSERVATIONS
FOR USE WITH H O PUB NO 606 C

VESSEL	STRANGER	MONTH	Oct.	YEAR	1957	TIME ZONE	PST
CRUISE	5710-S	SHEET NO	1 OF 5				

CONSEC. NUMBER	GREENWICH MEAN TIME		LATITUDE	LONGITUDE	DEPTH (Meter)		SEA SURFACE TEMP (Bucket)	WIND		AIR TEMP		BAROM (cm)	WEATHER (Tab 3)	CLOUDS		VIS (Tab 6)	SEA (Tab 7)	SWELL		BT INSTR NO	OBS INIT
	HOUR	DATE						DIR	SPEED	DRY BULB	WET BULB			TYPE (Tab 4)	AMT (Tab 5)			DIR	AMT		
H-1	0734	4	30 26.0	116 11.0	468		19 3	315	4	65 0	60 9	7405	02	6	6	8	2			78848	G
H-2	1015	4	30 20.0	116 23.0	1350		19.9	350	3	65.8	61.0	7405	02	6	3	8	2			78848	G
H-3	1340	4	30 10.0	116 43.0	2790		20.2	340	5	68.3	64.2	7395	02	6	2	8	3			78938	G
H-4	1925	4	29 50.0	117 24.0	3060		20.0	300	5	66.8	60.1	7455	01	—	0	8	3			78938	DB
H-5	0040	5	29 30.0	118 02.0	3060		20.4	325	5	62.2	61.4	7465	03	0	3	8	3			78938	DB

FORM 20 DCFG

Figure 2.12. Oceanographic log sheet for bathythermograph observations. (Courtesy University of California, Scripps Institution of Oceanography).

2.1.4.3. Neuston

It is advisable to include a neuston tow for larvae and juveniles for 10 minutes during the Bongo net tow. Larvae of several species of commercially-important pelagic fishes are known to occur in concentrations in the surface layer (Klawe, 1963; Sund and Richards, 1965; Parin, 1968; Zaitsev, 1970; Richards and Simmons, 1971). Their occurrence is mainly ephemeral, varying with stage of development, light, feeding, and oceanographic conditions (see review by Hempel and Weikert, 1972). Neuston samples can be collected with relatively small effort and they can provide valuable information on a number of kinds of fishes including tunas, billfishes, scombroids, and even some flatfishes. A rough check on presence or absence of eggs, larvae, and juveniles in the surface layer can be done with any kind of simple floating net which is towed at a speed of two knots. The mouth opening should cut the water surface and extend to about 10 to 50 cm deep. The tow should be operated aside of the ship and well clear of its bow wave and wake. Mesh size should be the same as in other ichthyoplankton sampling gear, i.e., about 0.3 or 0.5 millimeters. In some surveys, including the Cooperative Investigation of the Caribbean (CICAR), simple rectangular frame nets of 2 x 1 m or 1 x 0.5 m mouth aperture have been used. More sophisticated gear is now in use at several laboratories with the objective of sampling the near-surface layer in a more quantitative manner. The major difficulty in this respect is to control the depth of insertion of the net's mouth opening into the water and hence the amount of water filtered per meter of tow. The modified David-Neuston net (Hempel and Weikert, 1972), which is now recommended for international surveys such as the Cooperative Investigation of the Eastern Central Atlantic (CINECA), Sameoto's otter surface net (Sameoto and Jaroszynski, 1969), and various gears by Zaitsev (1970) have to be mentioned in this context.

2.1.4.4. Micronekton

Data on ichthyoplankton obtained from standard Bongo net samples can be usefully supplemented by larger nets with larger mesh for studying the larger, more agile larvae and juveniles. The objectives of these larger nets are to reduce the degree of avoidance, increase the total volume of water filtered, and reduce the amount of plankton from which the larger larvae and juveniles must be sorted. One such net has been designed for the National Marine Fisheries Service (NMFS) Marine Resources Monitoring Assessment and Prediction (MARMAP) program. The towing frame is the 6-foot Isaacs-Kidd midwater trawl (IKMT) with 2.89 m^2 mouth area, uniform 2 mm knotless mesh, with five times as much

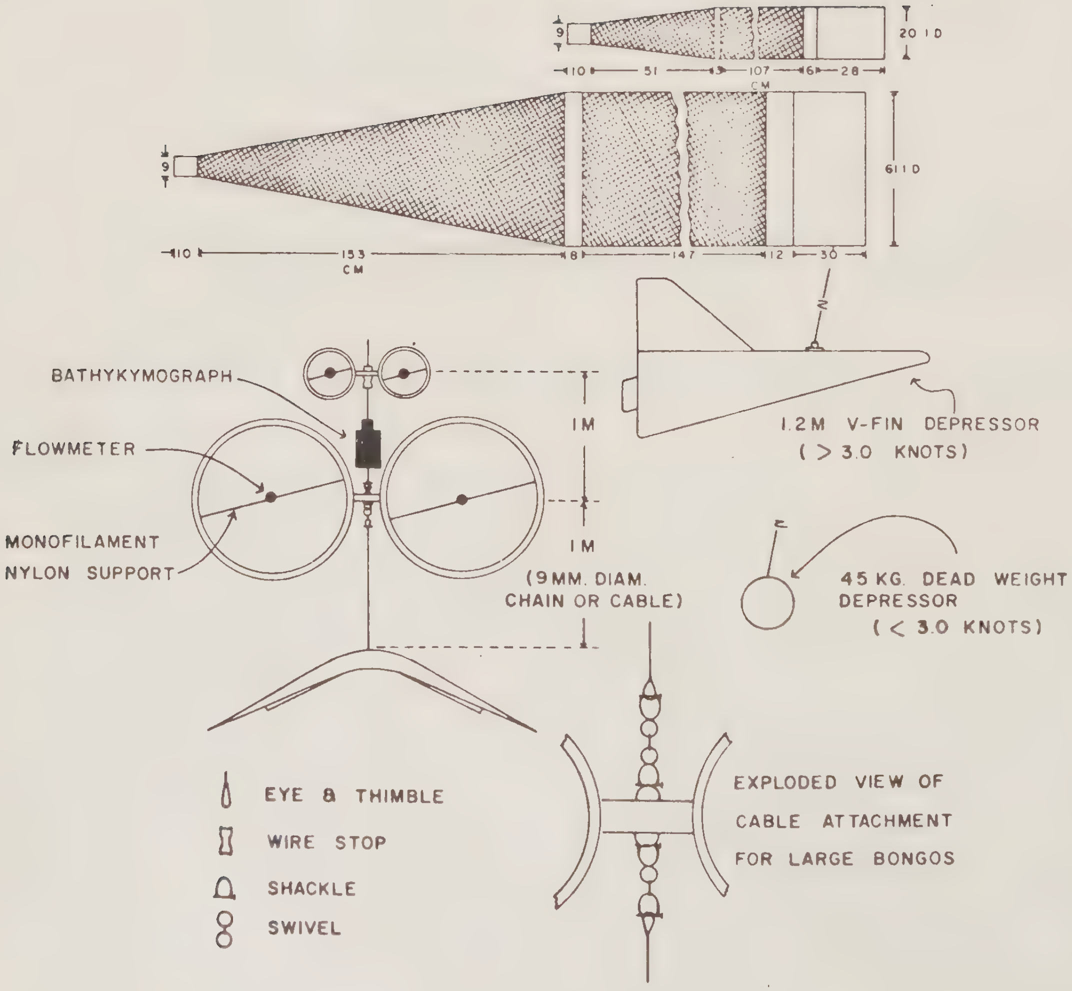
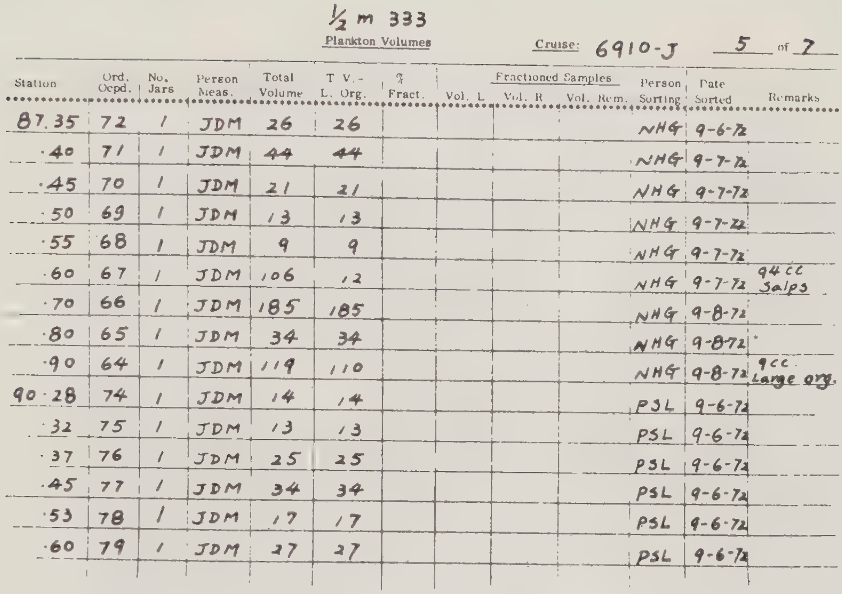

9
20 I D
10
51
3
107
CM
6
28
9
61 I D
10
153
CM
8
147
12
30
BATHYKYMOGRAPH
FLOWMETER
MONOFILAMENT
NYLON SUPPORT
I M
I M
(9 MM. DIAM.
CHAIN OR CABLE)
1.2 M V-FIN DEPRESSOR
(> 3.0 KNOTS)
45 KG. DEAD WEIGHT
DEPRESSOR
(< 3.0 KNOTS)
EYE & THIMBLE
WIRE STOP
SHACKLE
SWIVEL
EXPLODED VIEW OF
CABLE ATTACHMENT
FOR LARGE BONGOS

Figure 2.13. Paired Bongo net array with four mesh sizes; 0.505 mm, 0.333 mm, 0.250 mm, and 0.150 mm.



½ m 333

Plankton Volumes

Cruise: 6910-J 5 of 7

Station	Ord. Ocpd.	No. Jars	Person Meas.	Total Volume	T V.- L. Org.	% Fract.	Fractioned Samples Vol. L	Vol. R	Vol. Rem.	Person Sorting	Date Sorted	Remarks
87.35	72	1	JDM	26	26					NHG	9-6-72	
.40	71	1	JDM	44	44					NHG	9-7-72	
.45	70	1	JDM	21	21					NHG	9-7-72	
.50	69	1	JDM	13	13					NHG	9-7-72	
.55	68	1	JDM	9	9					NHG	9-7-72	
.60	67	1	JDM	106	12					NHG	9-7-72	94 cc Salps
.70	66	1	JDM	185	185					NHG	9-8-72	
.80	65	1	JDM	34	34					NHG	9-8-72	
.90	64	1	JDM	119	110					NHG	9-8-72	9 cc Large org.
90.28	74	1	JDM	14	14					PSL	9-6-72	
.32	75	1	JDM	13	13					PSL	9-6-72	
.37	76	1	JDM	25	25					PSL	9-6-72	
.45	77	1	JDM	34	34					PSL	9-6-72	
.53	78	1	JDM	17	17					PSL	9-6-72	
.60	79	1	JDM	27	27					PSL	9-6-72	

Figure 2.14. Plankton volume data sheet. (Modified from Kramer et al., 1972)

filtering area as mouth area. The present (1973) use of the net is in an oblique tow from 200 m to the surface filtering 13,000 m^3 of water at 4 knots towing speed. The duration of the tow is 35 minutes. All samples are taken at night. The early experimental work is being conducted in conjunction with a 75 m^2 otter board trawl with 4 mm mesh to discern the upper limits of effective sampling of fish larvae and juveniles in the 6-foot IKMT. The MARMAP IKMT is not designed for opening and closing at depth. The Tucker net, with square mouth opening, can be modified into an effective opening-closing micronekton net (Davies and Barham, 1969).

2.2. Laboratory Procedures

This section describes laboratory techniques employed in processing plankton samples, collected specifically for fish eggs and larvae, to be used for spawning biomass estimates. Determining the number and kind of fish eggs and larvae present in each sample is of primary interest. A secondary interest is the other plankton constituents as they relate to the well-being of the young stages of fishes, either as prey (food) or predators. The samples may also be used for other studies, e.g., the taxonomy of the various constituents, plankton community structure, indicator organisms, zoogeography, life history studies, etc., which are beyond the scope of this manual.

2.2.1. Plankton Volume Determinations

A measurement of wet plankton volume, determined by displacement, is made for each plankton sample soon after the samples are taken ashore. This data is recorded for each cruise on a plankton-volume data sheet (Fig. 2.14). The plankton volume measurement provides a rough measure of zooplanktonic biomass (Ahlstrom et al., 1969). It also has a practical value in the subsequent handling of the sample. Large samples may have to be aliquoted for sorting (Section 2.2.2.) and the size of the aliquot will often depend on sample size.

Two volumes (Fig. 2.14) are reported for each sample. The total volume includes everything in the sample except adult fishes, juvenile fishes, larger squids, octopi, and adult pelagic crabs (such as Pleuroncodes) which are not considered planktonic.

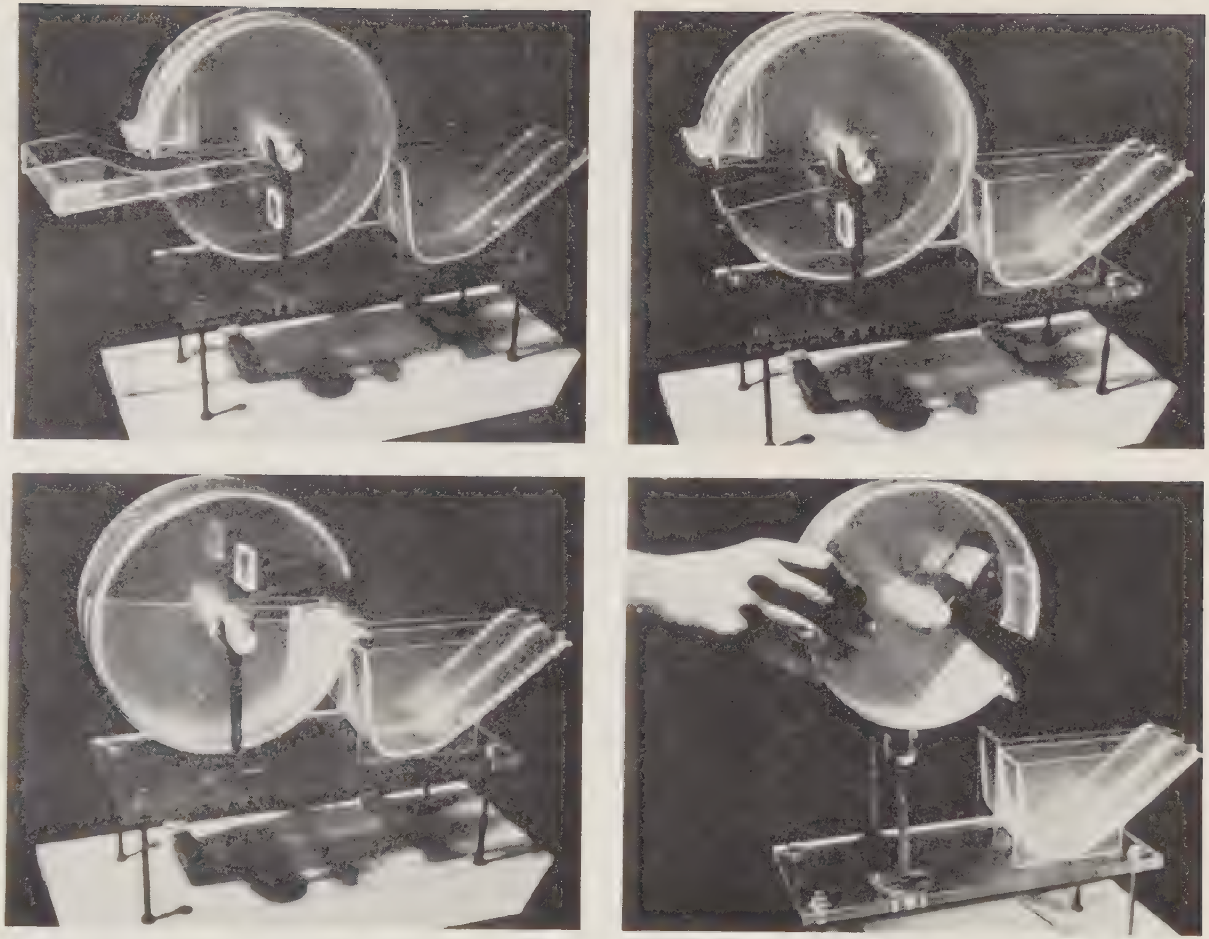


Figure 2.15. Folsom Plankton Splitter: a) septum inverted for pouring plankton sample into splitter; b) septum inverted for splitting; c) septum in place for divided sample; d) sample being poured into paired vessels. (Photos by K. Raymond, National Marine Fisheries Service, La Jolla, California.)

The total volume minus large organisms (Fig. 2.14) is the above volume minus the volume of large planktonic organisms such as large jellies or tunicates whose individual volumes exceed 5 ml.

The process of determining "wet" plankton volume by displacement is rather simple. The preserving liquid is removed from the plankton by pouring the sample through a draining cone, constructed of 0.333 mm Nitex. The plankton is retained in the cone until drainage of liquid from the cone diminishes to an occasional drop. The volume of the drained plankton is then determined by displacement in a graduated cylinder. Even after drainage, the sample will retain a considerable amount of interstitial liquid, usually between 30 to 40 percent of the total volume according to Ahlstrom and Thrailkill (1963). Usually no allowance is made for interstitial liquid; rather the total displacement volume of the drained "wet" sample is reported. The sample is returned to the original preserving liquid.

Additional information recorded on the plankton-volume data sheet (Fig. 2.14) includes station identification, the number of jars containing the sample, the proportions of fractioned samples, and the initials of the person who volumed the sample. Also, this data sheet is initialed by the sorter when the sample is checked out to be sorted (Section 2.2.3.).

2.2.2. Percentage of the Sample to be Sorted

It is recommended that total samples be sorted for fish eggs and larvae whenever possible, and that fractioning of samples be limited to those containing exceptionally large numbers of eggs and/or larvae or to samples with exceptionally large volumes of plankton material.

Several considerations should be weighed to determine whether an entire sample should be sorted for fish eggs and larvae, or only an aliquot. At times, it is desirable to sort only an aliquot for one category, usually eggs, and to sort the entire sample for the other, usually larvae. Sample size may or may not be a primary consideration for determining whether or not a sample should be aliquoted or completely sorted.

Eggs are often more abundant than larvae, and for many species are more aggregated so that occasionally, very large collections of eggs of the same species are obtained. For samples containing large numbers of eggs, it is usually advisable to split the sample into aliquots when sorting for eggs. The Folsom Splitter (Fig. 2.15) (McEwen, Johnson and Folsom, 1954) is a standard apparatus for dividing plankton samples into aliquot portions.

There are other considerations in sorting for larvae. One of the primary reasons for investigating larvae is to obtain information on the success of survival during the larval period. Such studies are postulated on the premise that the entire size range of larvae can be well sampled. Inasmuch as larger larvae may represent only a small percentage of the total number of larvae obtained of a species, it is usually necessary to sort entire samples in order to get an adequate representation of the larger-sized larvae.

2.2.3. Sorting Fish Eggs and Larvae from Plankton Samples

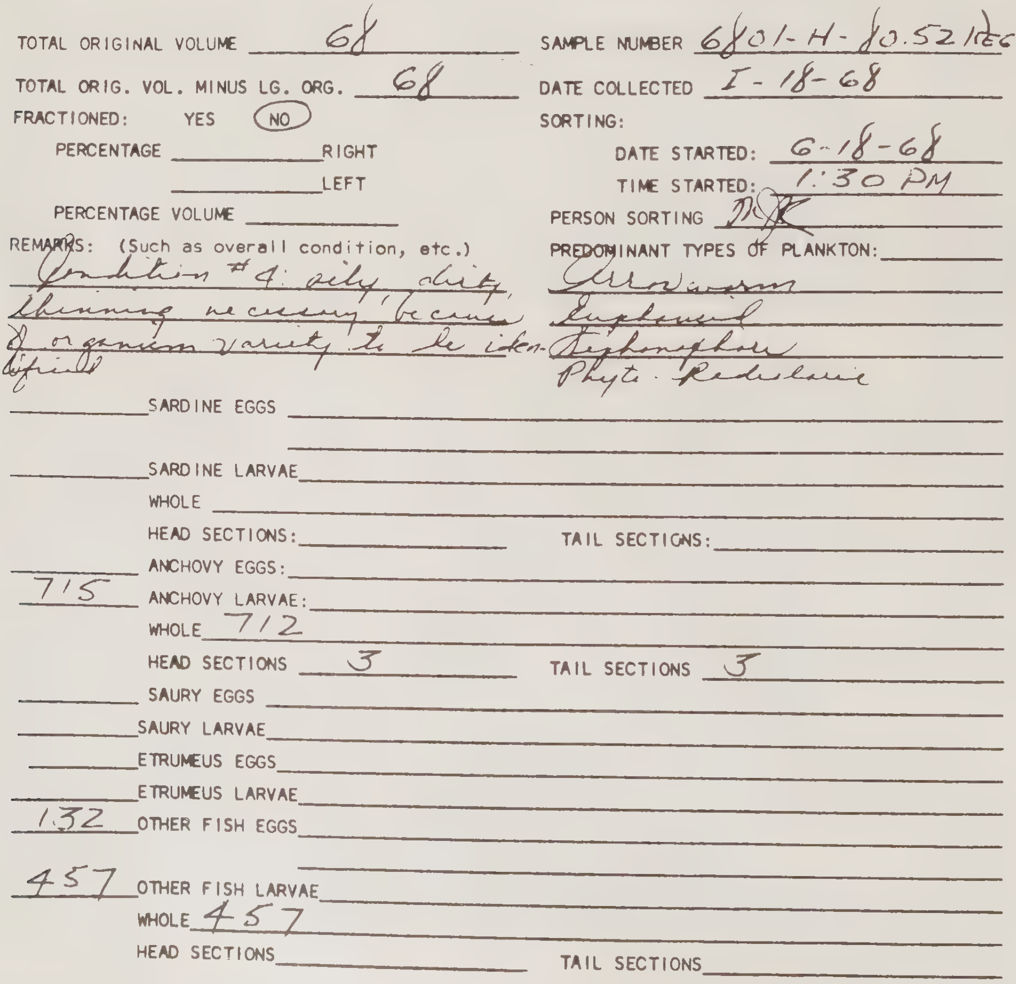
A sorter checks out a sample by initialing and dating the plankton-volume data sheet (Fig. 2.14). At this time a plankton sorter's work sheet (Fig. 2.16) is started which records the number of eggs and larvae removed from the sample. (Also refer to Section 2.2.4.).

Sorting is probably the step that requires the most time, e.g., one day per sample in the CalCOFI program. Before a sample is sorted, the preserving liquid (5% buffered Formalin) should be drained off because the formadehyde fumes, when breathed, can be irritating, even injurious to health. The sample can be sorted in a medium of fresh water or very weak Formalin solution. Precautions must be taken to prevent deterioration of the plankton material. If a sample has not been completely sorted during the day it was started, the unsorted plankton should be put back into 5% buffered Formalin during the night.

The best type of containers to use for sorting are small, e.g., Syracuse watch glasses or divided Petri dishes (Fig. 2.17). They permit cleaner, i.e., more complete, sorting of fish eggs and larvae than is possible from larger containers. Borgorov's counting tray is also widely used (Newell and Newell, 1963).

Sorting is usually done under a dissecting microscope (Fig. 2.17) at a magnification of about ten times (10x ocular, 1x objective). It is inadvisable to try to sort samples with the unaided eye.

A small amount of the sample to be sorted is poured into one of the glass dishes. Its contents are examined closely under the microscope. All fish eggs and larvae are removed with pipettes and fine quality stainless steel forceps, counted, and placed in appropriately labelled dishes (Fig. 2.17). The degree to which eggs and larvae are identified at this time will depend on the objectives of the survey and the training of the sorter (Sections 2.2.4., 2.2.5.). After the eggs and larvae have been sorted from a dish, its remaining contents are poured into a beaker labelled "Sorted". This process is repeated until the entire sample (or aliquot) has been sorted completely. The remaining plankton is then replaced in the original jar. The total number of fish eggs and larvae removed from the sample are recorded on the



TOTAL ORIGINAL VOLUME 68
SAMPLE NUMBER 6801-H-80.52 REG.
TOTAL ORIG. VOL. MINUS LG. ORG. 68
DATE COLLECTED I-18-68
FRACTIONED: YES [✓ NO]
SORTING:
PERCENTAGE ______ RIGHT
______ LEFT
DATE STARTED: 6-18-68
TIME STARTED: 1:30 PM
PERCENTAGE VOLUME ______
PERSON SORTING
REMARKS: (Such as overall condition, etc.)
Condition #4: oily, dirty, thinning necessary because of organism variety to be identified
PREDOMINANT TYPES OF PLANKTON:
Arrowworm
Euphausiid
Siphonophore
Phyto. Radiolaria

______ SARDINE EGGS ______
______ SARDINE LARVAE ______
WHOLE ______
HEAD SECTIONS: ______ TAIL SECTIONS: ______
______ ANCHOVY EGGS: ______
715 ANCHOVY LARVAE: ______
WHOLE 712
HEAD SECTIONS 3 TAIL SECTIONS 3
______ SAURY EGGS ______
______ SAURY LARVAE ______
______ ETRUMEUS EGGS ______
______ ETRUMEUS LARVAE ______
132 OTHER FISH EGGS ______
457 OTHER FISH LARVAE ______
WHOLE 457
HEAD SECTIONS ______ TAIL SECTIONS ______

Figure 2.16. Ichthyoplankton sorter's work sheet (From Kramer et al., 1972)

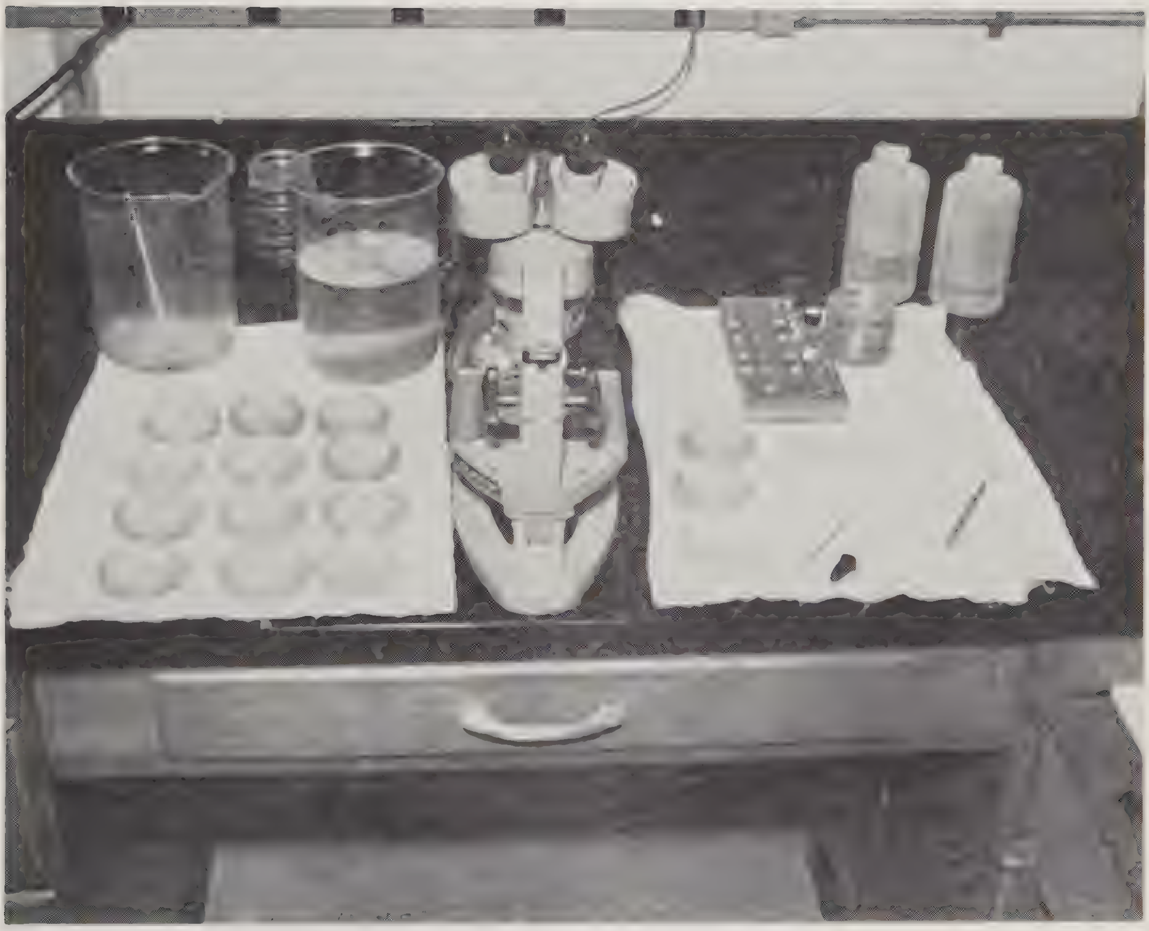
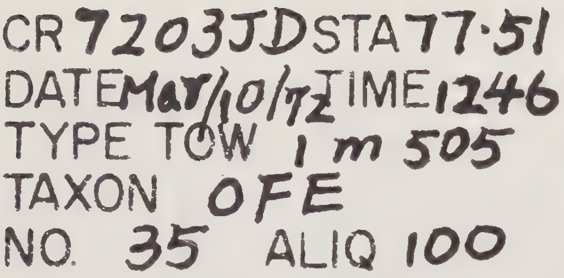


Figure 2.17. A laboratory sorting table. (From Kramer et al., 1972)



CR 7203JD STA 77·51
DATE Mar/10/72 TIME 1246
TYPE TOW 1 m 505
TAXON OFE
NO. 35 ALIQ 100

Figure 2.18. Label used inside vials of sorted and identified fish eggs and larvae.

plankton sorter's work sheet (Fig. 2.16.). The eggs and larvae are then stored in separate appropriately labelled (Fig. 2.18.) vials. For most samples, 2-dram (about 7 ml) vials are quite satisfactory. The preservative added to the larvae is 3 percent buffered Formalin in tap water, which has proved to keep eggs and larvae in good condition indefinitely. The type of screw cap recommended for the 2-dram glass vials is plastic with a vinyl insert that is self-sealing when firmly tightened on the vial (Fig. 2.19). This screw cap is much preferred to corks, rubber stoppers, or screw caps lacking the vinyl insert because it retards evaporation.

The goal of sorting should be to remove 100% of the fish eggs and larvae. Thus, it is essential to establish checks on the completeness of sorting samples. This requires that either samples selected at random be completely re-sorted by another person or a system be devised for the routine rechecking by a second sorter of each sample sorted. Note: It is firmly recommended that the sorting of a sample for fish eggs and larvae be completed before sorting is commenced on other taxa in the sample. Sorting of the other taxa can be used as a means of rechecking for ichthyoplankton.

2.2.4. Preliminary Identification, Enumeration, and Measurement of Fish Eggs and Larvae

Technicians who sort fish eggs and larvae from other plankton constituents also can be trained to recognize and separate eggs and larvae of selected families of fishes such as clupeids, engraulids, scombrids, scomberesocids, carangids, etc. To identify eggs of some fishes, the technicians will have to make measurements of diamater of eggs and of their oil globules, if present. Technicians, i.e., sorters, can be readily taught to separate engraulid larvae from clupeid larvae; however, they should not be expected to make subtle distinctions among clupeid larvae, for example, or among engraulid larvae when several species of either family are represented in the collections. This is a task for ichthyoplanktologists.

If the eggs and larvae of selected species are identified at the sorting level, these species are enumerated and recorded (Fig. 2.16) separately with the remainder being placed in the categories OFE (other fish eggs) and OFL (other fish larvae).

Before bottling, larvae of the selected species may be measured and the lengths recorded on a tabulation sheet (Fig. 2.20). The larval length (standard length) is estimated to the nearest half millimeter. The larvae are measured under a microscope by passing each individual over a glass slide which has a transparent plastic rule taped beneath it.

After the data on preliminary identification, enumeration, and measurement have been recorded on the proper data sheets (Figs. 2.16, 2.20), the eggs and larvae are bottled for storage (Sect. 2.2.6.). An appropriate label (Fig. 2.18) is placed in each vial and the sample is kept together as a unit. Identifications made at the sorting level are rechecked by more highly trained "identifiers" to assure quality. After all the samples from a cruise have been sorted, a plankton sorters' master sheet (Fig. 2.21) is compiled.

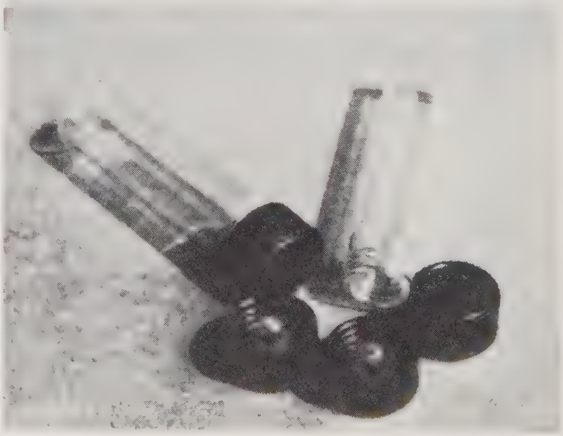
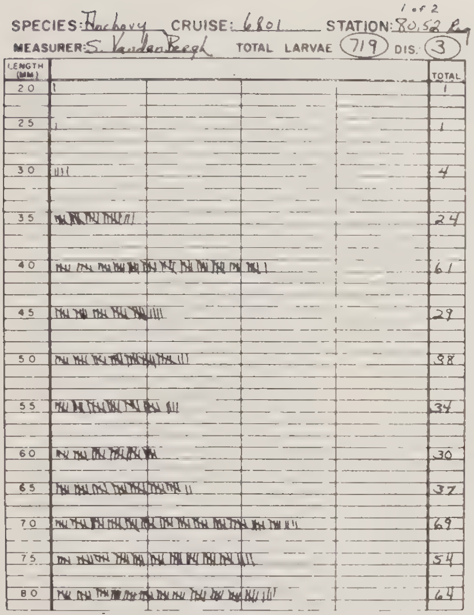


Figure 2.19. Two-dram (7 ml) glass vials and plastic caps used for storing sorted and identified fish eggs and larvae. (From Kramer et al., 1972)



1 of 2

SPECIES: Anchovy CRUISE: 6801 STATION: 80.52

MEASURER: S. VandenBergh TOTAL LARVAE 719 DIS. 3

LENGTH (MM)	TOTAL
20	1
25	1
30	4
35	24
40	61
45	29
50	38
55	34
60	30
65	37
70	69
75	54
80	64

Figure 2.20. Work sheet for tabulating measurements of fish larvae. (From Kramer, et al., 1972)

2.2.5. Final Identification of Fish Eggs and Larvae

The thoroughness with which collections of fish eggs and larvae are to be identified depends on the objectives of a survey and on personnel available for the work. The subject of identification is outside the scope of this manual. A bibliography of current research in this field is being prepared separately (FAO Fish.Circ.706)

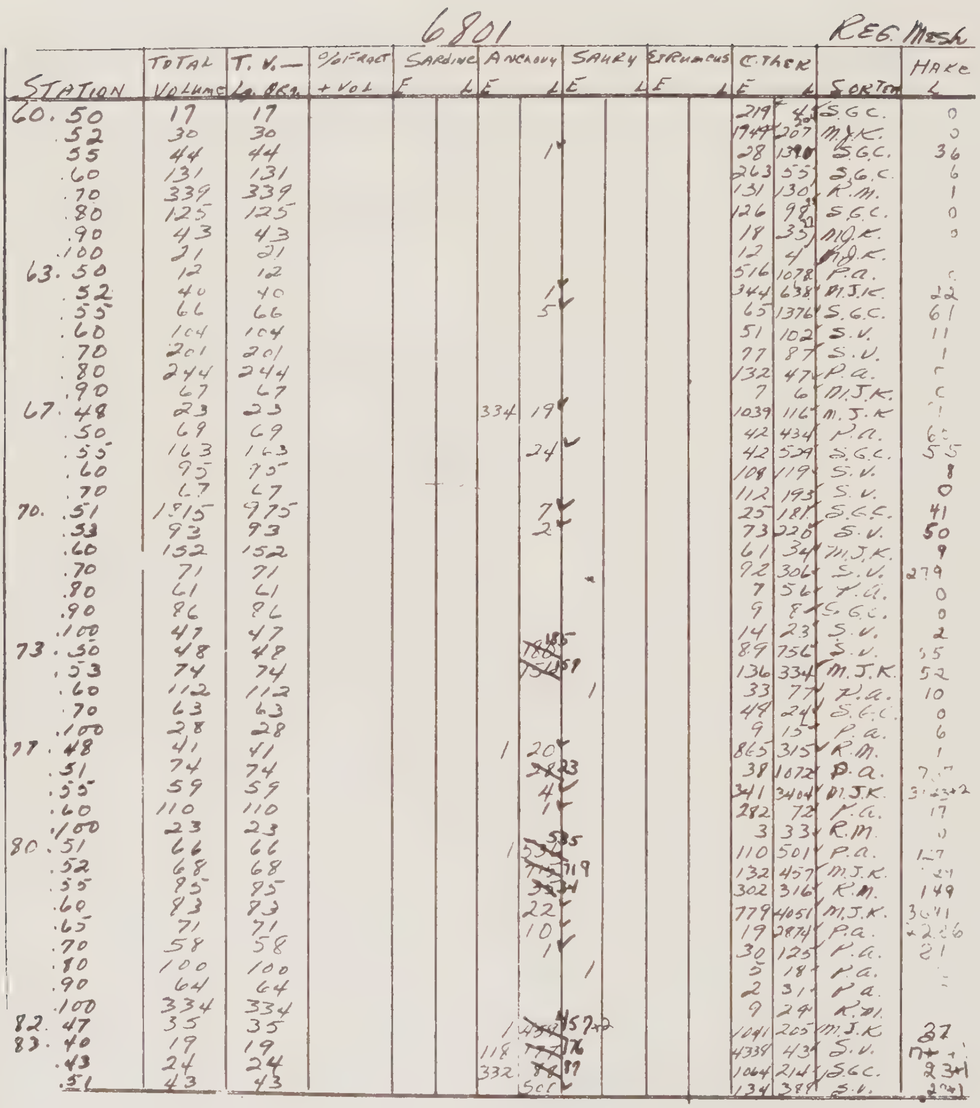
If surveys for fish eggs and larvae are designed to deal with only one or a few species whose eggs and larvae can be readily identified, the identification problem discussed below does not exist and the task of identification can be assigned to easily trained technicians who also do the sorting and enumerating (Sections 2.2.3. and 2.2.4.).

Often the problem of identifying fish eggs and larvae is not this simple. In many groups it is difficult to distinguish between larvae of closely related species, as for example between the larvae of albacore tuna (Thunnus alalunga) and yellowfin tuna (Thunnus albacares) (Matsumoto et al., 1972) or between larvae of clupeid species belonging to the same genus, such as Sardinella (Fagetti, 1970), or between most species of engraulid larvae, or between herring (Clupea harengus) and sprat (Sprattus sprattus), etc. The problem is further complicated if all fish eggs and larvae are to be identified and enumerated. In most situations, the problem of the initial identification of fish eggs and larvae should be entrusted to competent ichthyoplanktologists.

The development stages of pelagic fish eggs and larvae have yet to be described in literature for a majority of marine fishes. The state of our knowledge is not as "primitive", however, as the above statement would seem to indicate. Early life history stages have been described for perhaps less than 10 percent of marine fishes, but, fortunately, these belong to a large number of marine fish families. By using information already available in literature, the majority of fish larvae (say 95 percent) can be identified to the family level. Scorpaenid larvae, for example, can be readily identified to the family level; life history stages have yet to be published, however, for most genera and species of Scorpaenidae. Hence, working out the life history stages of the various genera and species within a family becomes the primary task of the trained ichthyoplanktologist. The quality of literature dealing with the life history stages of fishes ranges from excellent to miserable, with a much higher percentage of poor contributions than good ones.

It is important that ichthyoplankton scientists be generalists as well as specialists, i.e., that they have the training and knowledge to identify fish larvae in general. To be a generalist, there is no alternative but to work on identification of all constituents (eggs and larvae) from total samples.

The egg and larval stages of some groups of fishes are particularly difficult to identify, such as those of scombrids (particularly tunas), clupeids, engraulids. Those of some other groups are difficult because they contain many genera and/or species, such as scorpaenids, serranids, carangids, labrids, paralepidids, etc. Hence, specialists are needed to work out the life history stages of all difficult groups. The work on any difficult group is facilitated if comparative material is available from other areas or oceans. There is a great need for coordination of such studies on a worldwide basis, in order to prevent duplication of effort, to



6801 REG. MESH

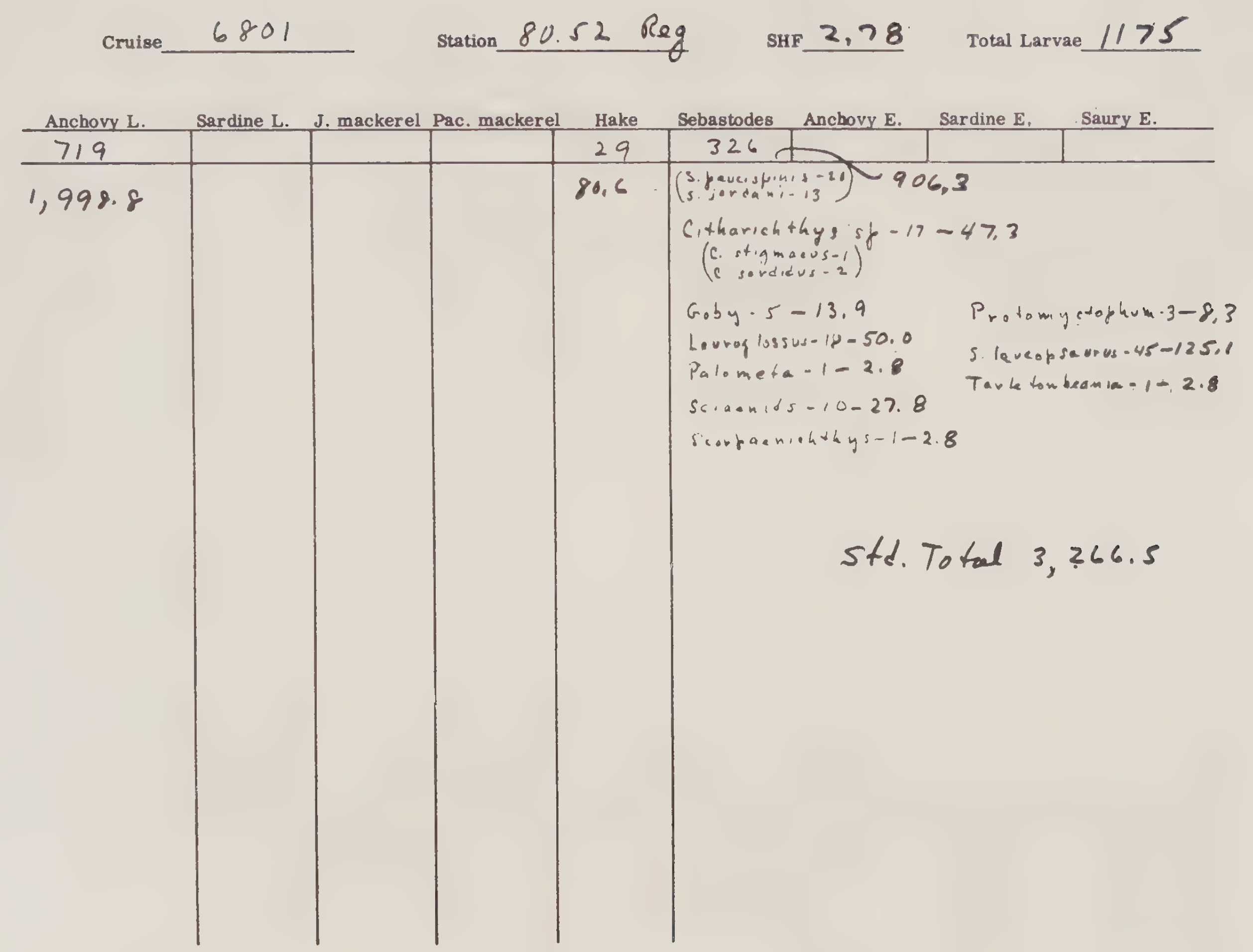
STATION	TOTAL VOLUME	T. V.— LG. ORG.	% OF FRACT + VOL	SARDINE E	SARDINE L	ANCHOVY E	ANCHOVY L	SAURY E	SAURY L	ETRUMEUS E	ETRUMEUS L	OTHER E	OTHER L	SORTER	HAKE L
60.50	17	17										219	45	S.G.C.	0
.52	30	30										1949	207	M.J.K.	0
55	44	44					1					28	1390	S.G.C.	36
.60	131	131										263	55	S.G.C.	6
.70	339	339										131	130	R.M.	1
.80	125	125										126	98	S.G.C.	0
.90	43	43										18	35	M.J.K.	0
.100	21	21										12	4	M.J.K.	
63.50	12	12										516	1078	P.a.	0
.52	40	40					1					344	638	M.J.K.	22
.55	66	66					5					65	1376	S.G.C.	61
.60	104	104										51	102	S.V.	11
.70	201	201										77	87	S.V.	1
.80	244	244										132	47	P.a.	[illegible]
.90	67	67										7	6	M.J.K.	0
67.48	23	23				334	19					1039	116	M.J.K.	[illegible]
.50	69	69										42	434	P.a.	[illegible]
.55	163	163					24					42	529	S.G.C.	55
.60	95	95										108	119	S.V.	8
.70	67	67										112	193	S.V.	0
70. .51	1315	975					7					25	181	S.G.C.	41
.53	93	93					2					73	220	S.V.	50
.60	152	152										61	34	M.J.K.	9
.70	71	71										92	306	S.V.	279
.80	61	61										7	56	P.a.	0
.90	86	86										9	8	S.G.C.	0
.100	47	47										14	23	S.V.	2
73.50	48	48					~~788~~ 185					89	756	S.V.	55
.53	74	74					~~751~~ 851					136	334	M.J.K.	52
.60	112	112						1				33	77	P.a.	10
.70	63	63										49	24	S.G.C.	0
.100	28	28										9	15	P.a.	6
77.48	41	41				1	20					865	315	R.M.	1
.51	74	74					~~28~~ 23					38	1072	P.a.	[illegible]
.55	59	59					4					341	3404	M.J.K.	3123+2
.60	110	110					1					282	72	P.a.	17
.100	23	23										3	33	R.M.	0
80.51	66	66				1	~~53~~ 535					110	501	P.a.	127
.52	68	68					~~775~~ 719					132	457	M.J.K.	[illegible]
.55	95	95					~~33~~ 34					302	316	R.M.	149
.60	83	83					22					779	4051	M.J.K.	3641
.65	71	71					10					19	2874	P.a.	+236
.70	58	58					1					30	125	P.a.	21
.80	100	100						1				5	18	P.a.	
.90	64	64										2	31	P.a.	
.100	334	334										9	24	R.M.	
82.47	35	35				1	~~439~~ 457+2					1041	205	M.J.K.	27
83.40	19	19				118	~~777~~ 76					4339	43	S.V.	[illegible]
.43	24	24				332	~~88~~ 89					1064	214	S.G.C.	23+1
.51	43	43					500					134	389	S.V.	[illegible]

Figure 2.21. Ichthyoplankton sorters' master sheet. (From Kramer et al., 1972)

facilitate exchange of comparative materials, to stimulate work on neglected groups, and to encourage development of new techniques.

Not all kinds of fish eggs and larvae are difficult to identify to genus or species. In some groups of fishes, eggs and larval characters can be superior to adult characters for making definitive identifications to the genus or species level. Obvious examples would include myctophid larvae (Pertseva-Ostroumova, 1964; Moser and Ahlstrom, 1970; Moser and Ahlstrom, 1972), bathylagid eggs and larvae (Ahlstrom, 1971), and paralepidid larvae (Ege, 1930, 1953, 1957).

The most comprehensive series of collections of fish eggs and larvae has been made by the California Cooperative Oceanic Fisheries Investigations (CalCOFI). For working up CalCOFI collections, the decision was made at the initiation of the program



Cruise 6801 Station 80.52 Reg SHF 2.78 Total Larvae 1175

Anchovy L.	Sardine L.	J. mackerel	Pac. mackerel	Hake	Sebastodes	Anchovy E.	Sardine E.	Saury E.
719				29	326			
1,998.8				80.6	(S. paucispinis-21 S. jordani-13) 906.3			

Citharichthys sp-17-47.3
(C. stigmaeus-1
C. sordidus-2)

Goby-5-13.9
Leuroglossus-18-50.0
Palometa-1-2.8
Sciaenids-10-27.8
Scorpaenichthys-1-2.8

Protomyctophum-3-8.3
S. leucopsaurus-45-125.1
Tarletonbeania-1-2.8

Std. Total 3,266.5

Figure 2.22. Fish egg and larva identification sheet. (From Kramer et al., 1972)

to identify all constituents to at least the family level, and all common kinds to genus or species. When this is done, the person making the identifications records the data on a special identification sheet (Fig. 2.22.). The collections so treated to date are in the neighborhood of 30,000, a clear demonstration that this approach is feasible. This information has permitted a critical evaluation of the fishery resources of the California Current region. It should be noted that some species are dealt with in more detail than others. For example, larvae are measured routinely for only a few important species, i.e., Pacific sardine, northern anchovy, jack mackerel, Pacific mackerel and recently Pacific hake. Most of the CalCOFI egg and larva data have been put on tape for computer handling. Standardization of data is now done by computer, as well as summary tables, distribution charts, statistical tests, etc.

2.2.6. Bottling, Storing and Curating Identified Collections of Fish Eggs and Larvae

After a collection of fish eggs and larvae has been identified, it is usually inadvisable to try to bottle each category of fish eggs or larvae separately. Hence, a decision has to be made as to which categories should be bottled separately, and which kept together as a unit.

It is advisable to establish a reference collection of identified fish eggs and larvae which would include not only eggs and larvae of important species, but eggs and larvae of as many kinds of fishes as can be identified with certainty. Specimens selected for the reference collection are, of course, bottled separately. The original identification sheet (Fig. 2.22) should note all specimens of eggs and larvae that are separately bottled for placement in the reference collection. Within the reference collection, eggs and larvae of fishes belonging to the same family are kept together as a unit, arranged alphabetically by genus and species. A phylogenetic arrangement of families can be utilized, or an alphabetical arrangement of families. The former is the more convenient arrangement for trained ichthyologists, the latter for persons with less scientific background.

Collections of eggs and of larvae of species under major study should be bottled separately for ready retrieval if necessary. The eggs are usually "staged" and/or "aged"; larvae are measured. Sometimes food studies are made on gut contents of larvae, etc.

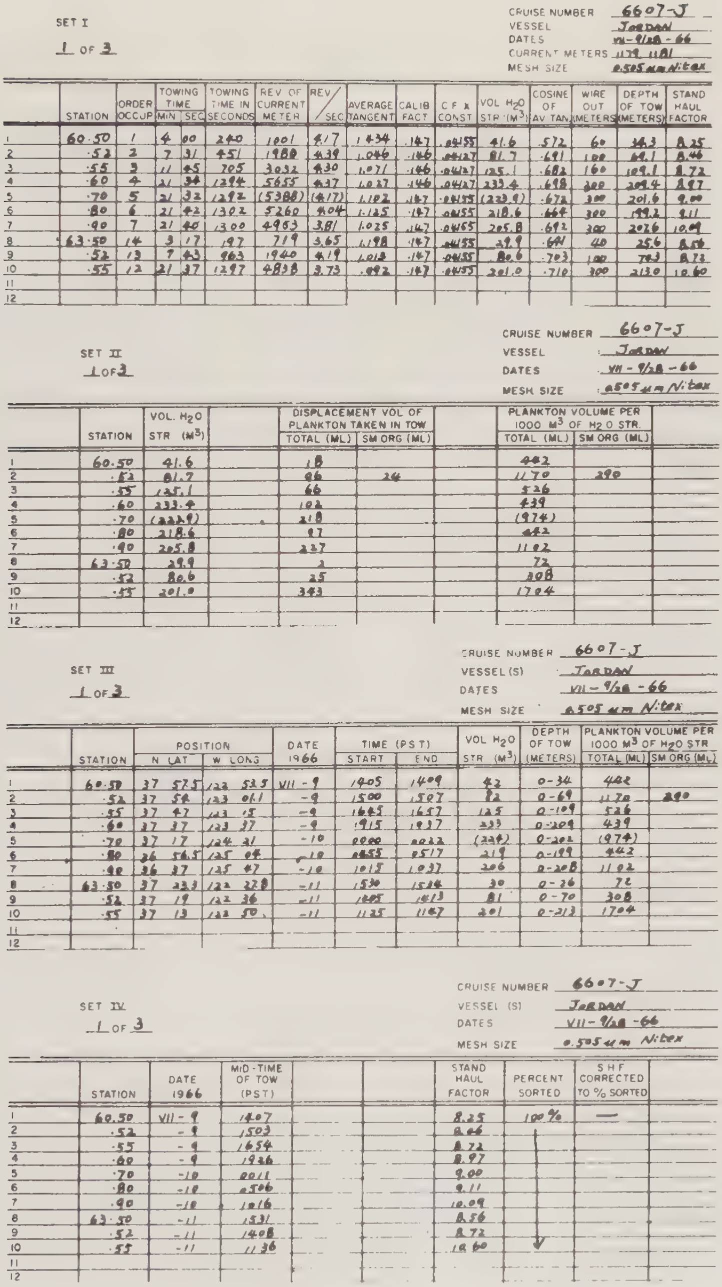
Eggs and larvae of species other than major species that are not separately bottled for the reference collection are best kept as units. Identified collections should be stored in an orderly manner, so that any given collection can be retrieved easily. For storing the 2-dram vials of eggs and larvae, a covered cardboard box having the dimensions length = 19 cm, width = 11.5 cm, depth = 7 cm is quite serviceable.

Samples stored in the above manner must be curated to prevent the samples from losing liquid by evaporation and eventually drying out. For ready retrieval of collections of fish eggs and larvae, such a storage system is most recommended. The curation time is well worth the effort. An alternative is to store samples in a bath of 3 to 5 percent Formalin. When so stored, the individual vials are usually stoppered with cotton. Perhaps the largest collection so curated is the Dana Collection (Carlesbergfondets at Charlottenlund Slot, Denmark), which utilizes 12-cm glass jars, 13.5 cm tall for storage of cotton-stoppered vials in a 5 percent Formalin bath. This is basically a museum storage technique, and cannot be recommended for collections that have to be consulted frequently.

2.3. Data Summarization

This section on data summarization considers only the recommended techniques for gathering the data collected on the ichthyoplankton survey for the estimation of spawning biomass. The analysis of errors in the process of gathering the data will be considered in Section 3, "Theoretical Considerations".

The end result of data summarization is to standardize the number of eggs or larvae in each plankton haul to the number under a unit area ($10m^2$ in this manual) of sea surface. This is a necessary prerequisite to estimating spawning biomass. Data forms used to assure good data summarization are shown in Fig. 2.23 and



SET I

1 OF 3

CRUISE NUMBER 6607-J
VESSEL JORDAN
DATES VII-9/11-66
CURRENT METERS 1179 1181
MESH SIZE 0.505 mm Nitex

	STATION	ORDER OCCUP	TOWING TIME MIN	TOWING TIME SEC	TOWING TIME IN SECONDS	REV OF CURRENT METER	REV/SEC	AVERAGE TANGENT	CALIB FACT	C F x CONST	VOL H_2O STR (M^3)	COSINE OF AV TAN	WIRE OUT (METERS)	DEPTH OF TOW (METERS)	STAND HAUL FACTOR
1	60.50	1	4	00	240	1001	4.17	1.434	.147	.0455	41.6	.572	60	34.3	8.25
2	.52	2	7	31	451	1980	4.39	1.046	.146	.0427	81.7	.691	100	69.1	8.46
3	.55	3	11	45	705	3032	4.30	1.071	.146	.0427	125.1	.682	160	109.1	8.72
4	.60	4	21	34	1294	5655	4.37	1.027	.146	.0427	233.4	.698	300	209.4	8.97
5	.70	5	21	32	1292	(5388)	(4.17)	1.102	.147	.0455	(223.9)	.672	300	201.6	9.00
6	.80	6	21	42	1302	5260	4.04	1.125	.147	.0455	218.6	.664	300	199.2	9.11
7	.90	7	21	40	1300	4953	3.81	1.025	.147	.0455	205.8	.692	300	202.6	10.09
8	63.50	14	3	17	197	719	3.65	1.198	.147	.0455	29.9	.641	40	25.6	8.56
9	.52	13	7	43	463	1940	4.19	1.012	.147	.0455	80.6	.703	100	70.3	8.72
10	.55	12	21	37	1297	4838	3.73	.992	.147	.0455	201.0	.710	300	213.0	10.60
11															
12															

SET II

1 OF 3

CRUISE NUMBER 6607-J
VESSEL JORDAN
DATES VII-9/11-66
MESH SIZE 0.505 μm Nitex

	STATION	VOL. H_2O STR (M^3)		DISPLACEMENT VOL OF PLANKTON TAKEN IN TOW TOTAL (ML)	DISPLACEMENT VOL OF PLANKTON TAKEN IN TOW SM ORG (ML)		PLANKTON VOLUME PER 1000 M^3 OF H_2O STR. TOTAL (ML)	PLANKTON VOLUME PER 1000 M^3 OF H_2O STR. SM ORG (ML)	
1	60.50	41.6		18			442		
2	.52	81.7		96	24		1170	290	
3	.55	125.1		66			526		
4	.60	233.4		102			439		
5	.70	(222.9)		218			(974)		
6	.80	218.6		97			442		
7	.90	205.8		227			1102		
8	63.50	29.9		2			72		
9	.52	80.6		25			308		
10	.55	201.0		343			1704		
11									
12									

SET III

1 OF 3

CRUISE NUMBER 6607-J
VESSEL(S) JORDAN
DATES VII-9/11-66
MESH SIZE 0.505 μm Nitex

	STATION	POSITION N LAT	POSITION W LONG	DATE 1966	TIME (PST) START	TIME (PST) END	VOL H_2O STR (M^3)	DEPTH OF TOW (METERS)	PLANKTON VOLUME PER 1000 M^3 OF H_2O STR TOTAL (ML)	PLANKTON VOLUME PER 1000 M^3 OF H_2O STR SM ORG (ML)
1	60.50	37 57.5	122 52.5	VII-9	1405	1409	42	0-34	442	
2	.52	37 54	123 01.1	-9	1500	1507	82	0-69	1170	290
3	.55	37 47	123 15	-9	1645	1657	125	0-109	526	
4	.60	37 37	123 37	-9	1915	1937	233	0-209	439	
5	.70	37 17	124 21	-10	0000	0022	(224)	0-202	(974)	
6	.80	36 56.5	125 04	-10	0455	0517	219	0-199	442	
7	.90	36 37	125 47	-10	1015	1037	206	0-208	1102	
8	63.50	37 22.3	122 27.8	-11	1530	1534	30	0-26	72	
9	.52	37 19	122 36	-11	1405	1413	81	0-70	308	
10	.55	37 13	122 50	-11	1125	1147	201	0-213	1704	
11										
12										

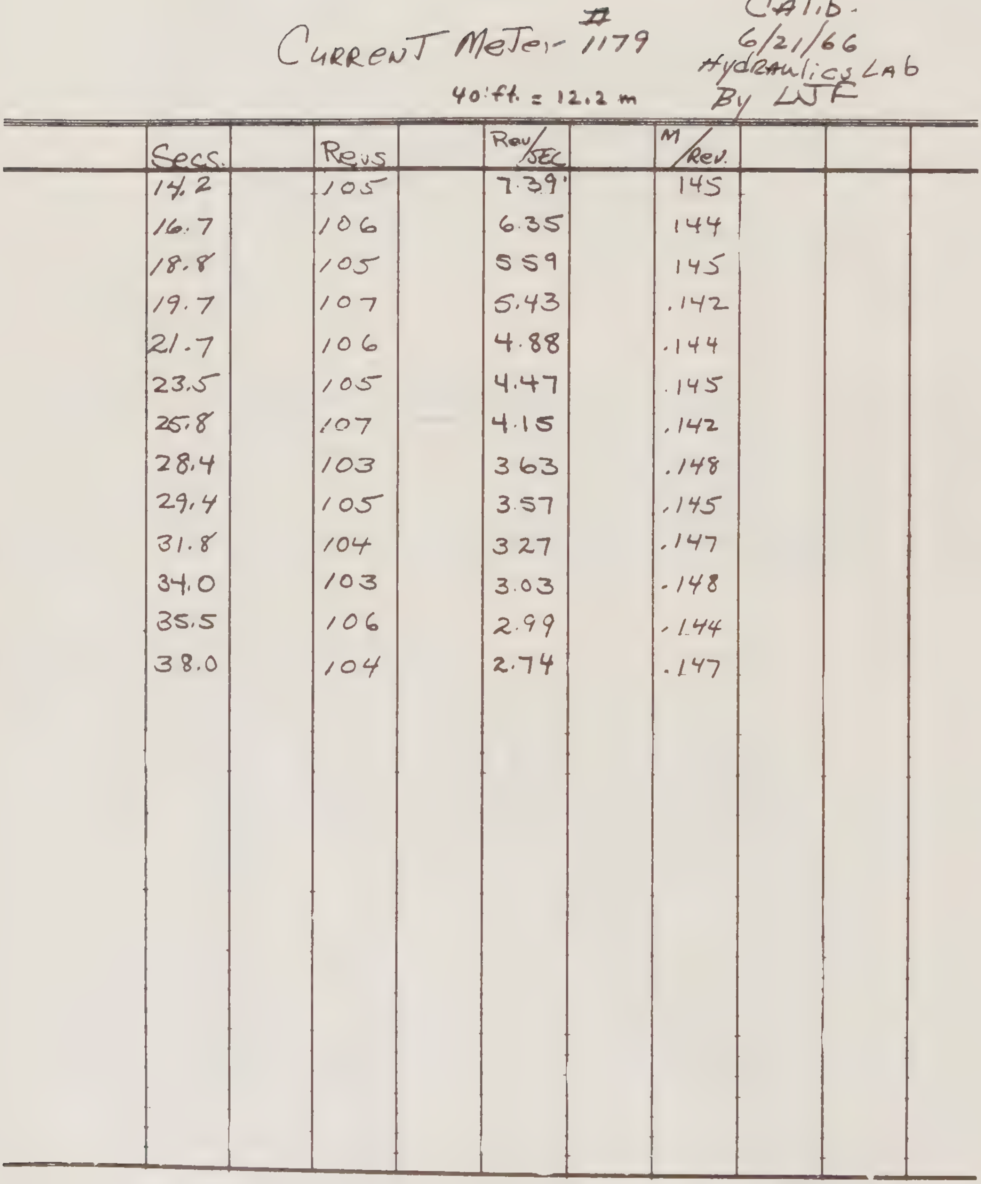
SET IV

1 OF 3

CRUISE NUMBER 6607-J
VESSEL (S) JORDAN
DATES VII-9/11-66
MESH SIZE 0.505 μm Nitex

	STATION	DATE 1966	MID-TIME OF TOW (PST)			STAND HAUL FACTOR	PERCENT SORTED	S H F CORRECTED TO % SORTED	
1	60.50	VII-9	1407			8.25	100%	—	
2	.52	-9	1503			8.46	↓		
3	.55	-9	1654			8.72			
4	.60	-9	1926			8.97			
5	.70	-10	0011			9.00			
6	.80	-10	0506			9.11			
7	.90	-10	1016			10.09			
8	63.50	-11	1531			8.56			
9	.52	-11	1408			8.72			
10	.55	-11	1136			10.60			
11									
12									

Figure 2.23. Forms used for data summarization. (Modified from Kramer *et al.*, 1972)



Current Meter #1179

Calib.
6/21/66
Hydraulics Lab
By LJF

40 ft. = 12.2 m

Secs.	Revs	Rev/SEC	M/Rev.
14.2	105	7.39	145
16.7	106	6.35	144
18.8	105	5 59	145
19.7	107	5.43	.142
21.7	106	4.88	.144
23.5	105	4.47	.145
25.8	107	4.15	.142
28.4	103	3 63	.148
29.4	105	3.57	.145
31.8	104	3 27	.147
34.0	103	3.03	.148
35.5	106	2.99	.144
38.0	104	2.74	.147

Figure 2.24. Record of tests for calibration of flowmeter #1179. (From Kramer *et al.*, 1972)

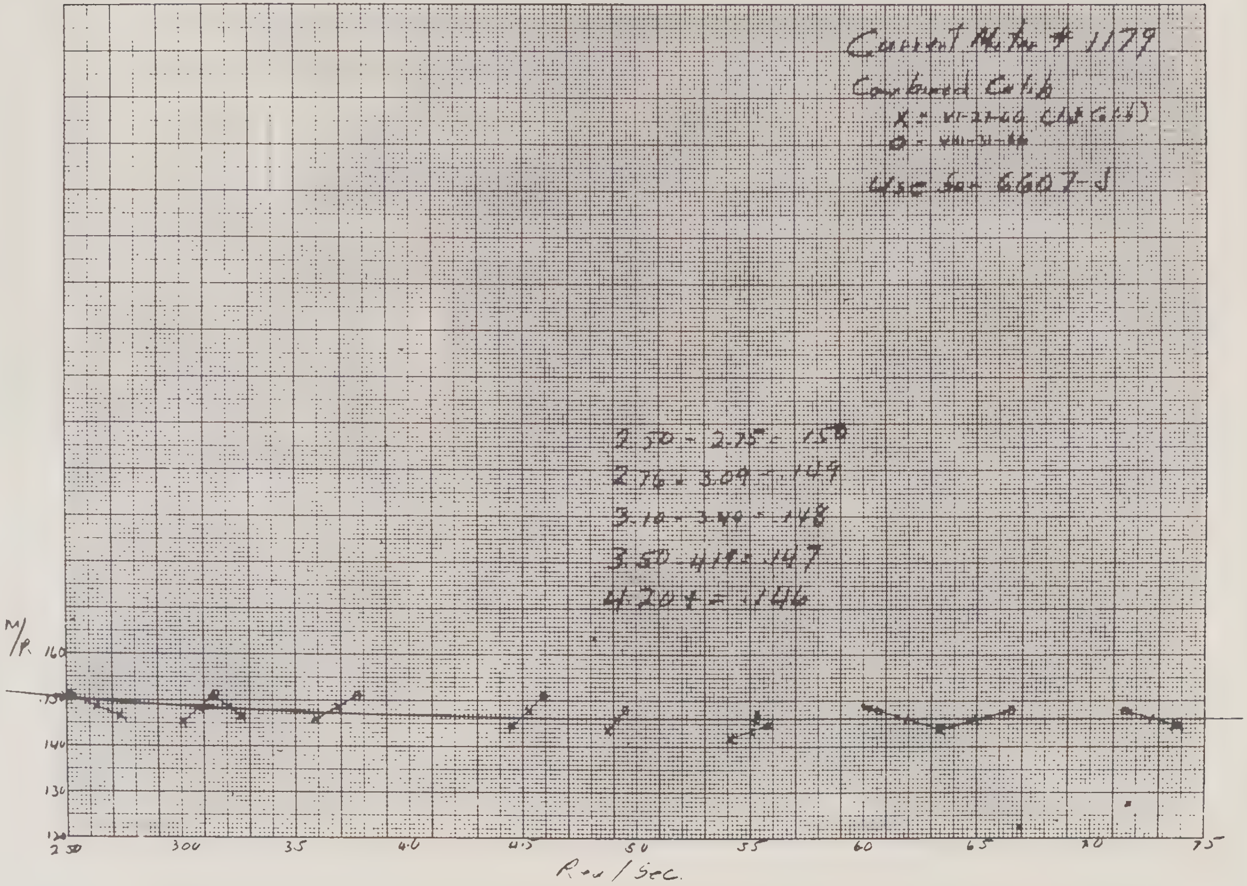


Figure 2.25. Flowmeter calibration curve. (From Kramer et al., 1972)

discussed in Section 2.3.4.

2.3.1. Flowmeter Calibration

To determine the standard haul factor for each tow requires that a calibrated flowmeter was placed in the mouth of each net and the flowmeter number and the revolutions made during each tow were accurately recorded (Item 12 on the plankton-tow data sheet, Fig. 2.8).

The calibration factor (f) is an expression of the number of meters the flowmeter travels during each revolution of the impeller (= m/rev). Different flowmeters are likely to differ from each other in this factor. The factor will not be the same for each towing speed for a single flowmeter. The same flowmeter may change its calibration factor gradually or may change it suddenly, if dropped, for example. For these reasons, each flowmeter to be used on a cruise is calibrated before each cruise, its performance is monitored during a cruise, and it is calibrated after each cruise. Spare flowmeters are taken on each cruise in case of loss or change in performance.

To calibrate a flowmeter, it is hauled or pushed through a measured distance of water at different speeds. The number of revolutions is recorded seperately for each test (Fig. 2.24). It is essential that uniform speed be maintained during each test. Calibration speeds should include speeds slow enough to define the friction point of each meter, and fast enough to bracket the range of speeds at which the flowmeter will be towed at sea.

The meters per revolution are then plotted against revolutions per second (Fig. 2.24) and form part of the calibration curve in Fig. 2.25. This graph, based on two calibration trials made before and after a cruise, provides an evaluation of the function of the flowmeter during the cruise. In this example, the calibration factors (f) are:

f_1 = 0.150 meters per revolution

f_2 = 0.149

f_3 = 0.148

f_4 = 0.147

f_5 = 0.146

Where the subscript number refers to individual ranges of speed:

1 = 2.50 to 2.75 revolutions per second

2 = 2.76 to 3.09

3 = 3.10 to 3.49

4 = 3.50 to 4.19

5 = 4.20

The latter value is good for all average towing speeds from 0.61 to at least 1.07 meters per second. The lowest usable average towing speed for this meter is 0.38 meters per second. Flowmeters are limited in performance at lower speeds due to proportionate increase in friction. The speed at which the meter stops is called the friction point. For the type of plankton tow recommended in this manual, flowmeters with friction points at or above 0.55 meters per second should be repaired or discarded.

2.3.2. Estimation of Missing Flowmeter Values

If a flowmeter value (number of revolutions) is missing from the plankton tow data sheet (Fig. 2.8), or if a recorded flowmeter value is obviously incorrect, it is possible to make an

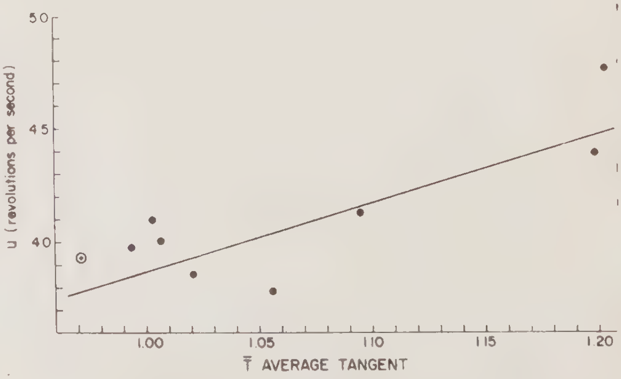


Figure 2.26. Regression line used to estimate a missing flowmeter reading (circled dot) for a particular flowmeter on a particular cruise, given average tangent for the tow in question and for other tows made with the same meter.

Table 2.1. Worksheet for calculation of the average tangent from the wire angles recorded each 10 meters of wire recovered (See Figure 2.8)

i	Θ	$\tan \Theta$
1	49°	1.1504
2	48	1.1106
3	47	1.0724
4	46	1.0355
5	47	1.0724
6	48	1.1106
7	48	1.1106
8	47	1.0724
9	47	1.0724
10	47	1.0724
11	46	1.0355
12	46	1.0355
13	48	1.1106
14	48	1.1106
15	46	1.0355
16	45	1.0000
17	47	1.0724
18	48	1.1106
19	48	1.1106
20	46	1.0355
21	45	1.0000
22	47	1.0724
23	49	1.1504
24	48	1.1106
25	46	1.0355
26	45	1.0000
27	46	1.0355
28	47	1.0724
29	45	1.0000
30	50	1.1918
SUM		32.2051
AVERAGE		1.0734

estimate of the missing value. The estimate is based on the average of all the wire angle readings made during the tow in question.

If a ship tows somewhat faster than usual, the wire angle will tend to be higher and the revolutions per second will also respond with an increase in rate. Consequently, a linear regression (Fig. 2.26) of the average tangent ($\bar{T}$) (Table 2.1 and Section 2.3.3.) and revolutions per second (u) based on other tows made by the same flowmeter may allow an adequate estimate of the number of revolutions for the tow in question. The precision of the estimate will be in part dependent on the number of tows taken with the same meter, and also on the technical quality of the tow records.

The least-squares method is used to calculate the regression line. The independent variable ($\bar{T}$) and the dependent variable (u) are listed in pairs (Table 2.2). The regression line, in this example, is described by the equation

$$u = 2.998\ \bar{T} + 0.874 \quad (r = 0.87\ ;\ r^2 = 75\%)$$

If the average tangent of the tow in question is 0.971 (Table 2.2), the estimated value of u is 3.79 revolutions per second.

2.3.3. Equation of Standardization

The basic equation of standardization is

$$C = 10\ (a^{-1}b^{-1}c\ d)$$

"C" is the number of eggs or larvae beneath a unit sea surface area (10 square meters in this case); "a" is the area of the mouth of the bongo net in square meters; "b" is the length of the tow path in meters; "c" is the number of eggs or larvae in the sample; and "d" is the maximum depth of tow in meters.

The value "a" is derived from the equation for a circle which is 60 cm in diameter (0.3 m radius);

$$\begin{aligned} a &= \pi r^2 \\ &= 3.141\ \ (0.3)^2 \\ &= 0.2827 \end{aligned}$$

The value "b" is derived from the calibrated flowmeter:

$$b = f\ r$$

"f" is the calibration factor in meters per revolution (m/rev) for a given flowmeter at a given number of revolutions per second (Section 2.3.1.); and "r" is the number of revolutions of the flowmeter during the tow. For example, in Fig. 2.23, Set I, Line 6

$$\begin{aligned} b &= 0.147\ (5260) \\ &= 773 \end{aligned}$$

The value "d" is determined from the tow data by the equation;

$$d = W \cos\ (\tan^{-1} \bar{T})$$

"W" is the maximum length of wire out in meters (m); this is usually determined by a meter block in the towing winch system (Section 2.1.2.2.) and is recorded on the tow data sheet (Fig. 2.8); "$\bar{T}$" is the average tangent of the wire angle taken at 30 second intervals (Fig. 2.8) during the recovery phase of the plankton tow;

$$\bar{T} = \frac{1}{n} \sum_{i=1}^{n} \tan \theta^{i}$$

and "θ" is the angle at each reading of the wire from the plankton tow data sheet (Fig. 2.8, Table 2.1). For example, (Fig. 2.23, Set I, Line 6)

$$\begin{aligned} d &= 300\ (0.664) \\ &= 199 \end{aligned}$$

Thus, for this example (Fig. 2.23, Set I, Line 6) "a" is 0.2827; "b" is 773; and "d" is 199. If 50 larvae (c=50) were taken in the sample, the solution to the equation would be

$$\begin{aligned} C &= 10\ \left(\frac{1}{0.2827} \times \frac{1}{773} \times 50 \times 199\right) \\ &= 455\ \text{larvae per 10 m}^2\text{ sea surface.} \end{aligned}$$

2.3.4. Data Forms Used for Standardization

The derivation of the equation of standardization (Section 2.3.3.) is not necessarily the same way the data become available or are needed. For sets of summary data sheets (Fig. 2.23) are used to assure the completeness and accuracy of organization of the data.

Set I (Fig. 2.23) summarizes the data from the plankton tow data sheet. Column 1 (in all four sets) is the station number. Column 2, which gives the order in which the station was occupied, comes from the "Captain's sheets" (Fig. 2.2). The order

Table 2.2. Worksheet for estimation of missing flowmeter readings by the method of least squares (regression).

TOW ORDER	AVERAGE TANGENT (T)	REVOLUTIONS PER SECOND (u)
1	1.243	4.76
2	0.971	3.79*
3	1.003	4.10
4	1.067	4.01
5	1.095	4.13
6	1.021	3.86
7	0.994	3.98
8	1.056	3.78
9	1.199	4.39

* estimated value

occupied is used to trace back faults in flowmeters (e.g., malfunction) and nets (e.g., clogging) which affect entire sequences of tows. Column 3 is the duration of tow (towing time) and is recorded in minutes and seconds on the tow data sheet (Fig. 2.8). Column 4 changes this value to seconds. The number of revolutions of the flowmeter is taken from the original tow data sheet and recorded in column 5. Column 6 lists the revolutions per second which is calculated by dividing the value in column 5 by the value in column 4. Revolutions per second is used to determine the calibration factor for the flowmeter (Section 2.3.1.). Column 6 is also monitored for high values to detect a cause of extrusion of small eggs and larvae. Column 7 is the average tangent derived from the original tow data sheet by converting the angle readings to tangents, adding them, and dividing by the number of readings (Table 2.1.). This value is rounded off to three places. It is used to determine the maximum depth of tow. The average tangent may also be used to estimate missing readings for a flowmeter which has been used for a series of tows on the same cruise (Sect. 2.3.2). Flowmeter calibration factors (Section 2.3.1) are recorded in column 8 and are read from the calibration curve (Fig. 2.25) derived for each flowmeter for each cruise at the rate of speed in column 6. In column 9 the mouth area of the net is multiplied by the calibration factor for use in determining the volume of water strained (filtered). In column 10 the volume of water strained is obtained by multiplying column 9, which is in m^3 per revolution, by column 5, which is in revolutions. In column 11 the cosine of the angle $\tan^{-1} \overline{T}$ is recorded for use in estimating the maximum depth of tow. This value provides a better estimate of the maximum depth of tow than the cosine of the angle with maximum wire out. Column 12, wire out is obtained from the original tow data sheet and is multiplied by the cosine of the angle $\tan^{-1} \overline{T}$ (column 11) to estimate the depth of tow (column 13). Column 14, the standard haul factor, is obtained by dividing column 13 by column 10 and multiplying the answer by 10. The standard haul factor multiplied by the number of eggs or larvae in the sample gives the number of eggs or larvae per 10 m^2 of sea surface.

Set II (Fig. 2.23) takes the information in Set I and the plankton sample displacement volume (Section 2.2.1.) and corrects the values to cubic centimeters of plankton per $1000m^3$ of water strained. The values for volume of plankton may be used to estimate the sorting time for the sample.

Set III (Fig. 2.23) is the summary of plankton volumes in a form which may be published. It lists the actual station position from the "Captain's sheets" (Fig. 2.2) and the mid-time of tow from Set I. Since the normal tow is about 20 minutes long, the data from the original tow data sheet (Fig. 2.8) are only recorded to within 5 minute accuracy. This information is used primarily for the study and correction of the day-night difference in plankton volume and numbers of larvae. Other

Table 2.3 Basic data table for assembly of regional data to be used in making census estimates. Numbers represent sardine larvae per 10 m^2 sea surface (C , Section 2.4) for each station on each cruise. "0" indicates no larvae of this species were taken. "-0" indicates the station was not occupied.

STATION	CRUISE					
	01	02	04	05	07	10
3.1	5	356	83	3	9	0
3.2	-0	96	5	0	22	0
3.3	0	14	36	6	21	0
3.4	0	0	0	0	3	0
4.1	0	0	0	0	3	0
4.2	-0	0	6	3	35	3
4.3	-0	0	43	-	90	13
4.4	-0	-0	0	0	12	0
5.1	-0	0	0	3	16	0
5.2	3	49	3	6	0	5
5.3	0	0	4	0	3	0
5.4	0	0	4	0	0	0
NUMBER OF STATIONS OCCUPIED (N)	7	11	12	12	12	12
NUMBER OF STATIONS WITH LARVAE (N_L)	2	4	8	5	10	3
NUMBER OF LARVAE (ΣC)	8	515	184	21	214	21
ΣC^2	34	138,549	10,136	99	10,758	203
$\Sigma \ln C$	1.176	7.370	8.267	2.988	10.832	2.290
$\Sigma (\ln C)^2$	0.716	14.610	10.820	1.894	13.962	1.957

Table 2.4. Statistical summary table of regional data derived from basic data in Table 2.3. (Area factor = 3.29 x 10^9)

CRUISE	N	N_L	ΣC	$\bar{C}$	S_C	$\overline{\ln C}$	$S_{\ln C}$	F	P	$L \times 10^9$
01	7	2	8	4.0	1.41	.588	.157	1.3	.286	4
02	11	4	515	128.75	155.18	1.843	.586	2.0	.364	154
04	12	8	184	23.00	29.04	1.033	.570	1.6	.667	50
05	12	5	21	4.20	1.64	.598	.165	1.2	.417	6
07	12	10	214	21.40	26.20	1.083	.498	1.4	.833	59
10	12	3	21	7.00	5.29	.763	.323	1.5	.250	6

Table 2.5. Statistical summary table of regional data derived from data in Tables 2.3. and 2.4.

SEASON	N	N_L	ΣC	$\bar{C}$	S_C	$\overset{n}{\overline{\ln C}}$	$S_{\ln C}$	F	P	$L \times 10^9$
Winter	18	6	523	87.17	136.37	1.424	.794	2.1	.333	96
Spring	24	13	205	15.77	24.16	1.645	.497	1.4	.542	28
Summer	12	10	214	21.40	26.20	1.083	.498	1.4	.833	59
Fall	12	3	21	7.00	5.29	.763	.323	1.5	.250	6
TOTAL										189

data columns are from Set I and Set II directly.

Set IV (Fig. 2.23) is used by the fish egg and larva "identifiers" to record sample data on the identification sheet (Fig. 2.22), e.g., standard haul factor, mid-time of tow, and percent of sample sorted.

2.4. Census Estimate (Larval Index)

To arrive at final census estimates, the spawning area and the survey season are divided into units which serve as pooled data areas. This allows a conservative estimate of precision and furnishes a concise summary of each year's spawning activity within each region. Data from the pooled area may furnish insight into changes in the allocation of sampling effort to maximize precision per unit cost for a target species (the primary species under study).

If it has been determined, for example, that the sample survey will be conducted over the four quarters of the year (1985) with two cruises each quarter in the spawning season and one cruise each quarter out of the normal spawning season, the stations close to each other may be grouped regionally and seasonally. If, for this example, the region of pooling (region #5) is 120 by 80 nautical miles and contains three lines of stations with four stations distributed along each line, the data for fish larvae may be assembled as shown in Table 2.3. At the base of each column, several sets of numbers have been calculated for analysis and inspection. They are the number of stations occupied (N), the number of stations at which sardine larvae occur (N_L), the total number of larvae taken in the region during the cruise

$$\Sigma C = \sum_{i=1}^{N} C_i$$

the sums of the squares of the numbers of larvae

$$\Sigma C^2 = \sum_{i=1}^{N} C_i^2$$

the sums of the logarithms of the numbers of larvae

$$\Sigma \ln C = \sum_{i=1}^{N} \ln C_i$$

and the sums of the squares of the logarithms of the numbers of larvae

$$\Sigma (\ln C)^2 = \sum_{i=1}^{N} (\ln C_i)^2$$

It is essential that these basic data are available for inspection so that questions arising in the interpretation can be traced to the original data.

These basic data (Table 2.3) are then summarized (Table 2.4). The original quantities N, N_L, and C are retained and the following quantities are calculated:

$$\overline{C} = \frac{\Sigma C}{N_L}$$

The mean number of larvae per positive station; and

$$S_C = [(\Sigma C^2 - N_L \overline{C}^2) / (N_L - 1)]^{\frac{1}{2}}$$

the standard deviation of the number of larvae per positive station; "$\overline{\ln C}$" the mean of the logs of larvae per positive station; "$S_{\ln C}$" the standard deviation of the logs of larvae per positive station; and "F" the error factor for the positive stations. "P" is the proportion of the stations which are positive (an estimate of the proportion of the sea surface underlain by larvae); and, "L", the larval index, is the regional census estimate of the number of larvae in this time period, which in the given example is

$$L = 3.29 \times 10^9 \ (P \ \overline{C})$$

where the factor 3.29×10^9 represents the number of 10 m^2 areas within the pooled region which in this case is 120 x 80 nautical miles.

Table 2.6. Total survey summary ($Lx10^9$) by years and regions.

YEAR	REGION									TOTAL
	1	2	3	4	5	6	7	8	9	
1978	84	321	204	439	250	131	1376	269	119	3193
1979	37	179	127	497	381	355	254	129	0	1959
1980	5	216	57	430	69	47	735	147	0	1706
1981	18	226	4	579	24	3	268	15	0	1137
1982	161	173	6	564	3	0	454	25	67	1453
1983	128	90	4	288	0	0	252	160	0	922
1984	187	120	70	374	181	5	406	152	11	1506
1985	36	35	6	99	189					

Table 2.7. Worksheet for comparing an independent biomass estimate with the larval index.

YEAR	BIOMASS ESTIMATE x 10^3 Tons	LARVAL INDEX x 10^9
1978	1336	3193
1979	850	1959
1980	586	1706
1981	424	1137
1982	562	1453
1983	380	922
1984	(593)*	1506

*estimate based on larval index

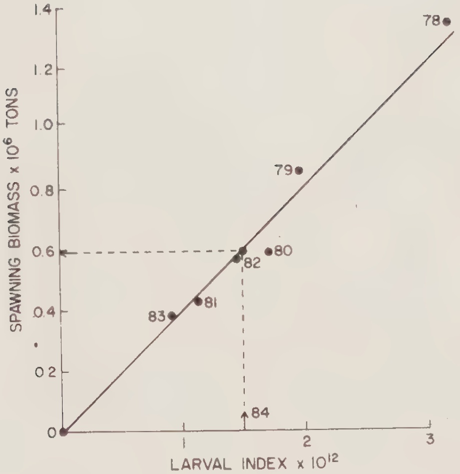


Figure 2.27. A scatter-plot of the relationship between spawning biomass and the larval abundance index. Numbers indicate years, e.g., 78=1978, etc.

Many of the factors displayed in Table 2.4 are used to assist in the evaluation of data. The cruises in this example do not represent equal periods of time, therefore, a further pooling of stations in time must be accomplished for the first two pairs of cruises. In Table 2.5, the two winter and spring cruises have been pooled and the regional census estimate of the number of larvae in the entire region in this time period has been obtained. This census estimate is an index of spawning intensity and coverage for this year in this region.

The larval index for region #5 in 1985 (total in Table 2.5) has been incorporated into the total survey summary in Table 2.6. This larval index can be used by itself to monitor changes in spawning biomass. The reliability of the larval index for such use is exemplified in Figure 1.2 when compared with two other independent estimates of biomass of the Pacific mackerel. The larval index can also be used in conjunction with other data to make instantaneous spawning biomass estimates. (Sections. 2.5, 3.6.)

2.5. Estimating the Spawning Biomass

One way to estimate the spawning biomass of the current population is by using the larval index of abundance. Other methods of making spawning biomass estimates from ichthyoplankton surveys are discussed in Section 3.6 along with problems involved in using them.

The method described here involves comparison of the larval index with another independent estimate of species abundance. This other estimate could be made, for example, by correlating the age composition of the stock with fishing effort and thus determining the number of fish in each age class as described by Murphy (1966). The larval index, when used in conjunction with Murphy's estimate, can make up for a generation of lag time and provide an estimate of the current spawning biomass.

A hypothetical example of this method of estimating biomass is provided in Table 2.7 and Figure 2.27. In this example, the larval index (total regional census estimate in Table 2.6.) is available from 1978 through 1984. The other independent estimate (Murphy, 1966) of fish biomass (Table 2.7) is available only through 1983. A linear relationship exists between these two estimates in the form of the equation:

$$B_s = 0.436\ L - 63.98\ (r = .989;\ r^2 \approx 98\%)$$

"B" is the spawning biomass of sardines, "L" is the larval index, "r" is the correlation coefficient, and "r^2" is the first estimate of the degree of dependence of spawning biomass on larval index. This equation provides a method of relating previous quantities of fish biomass with larva abundance in a way that can be used to estimate current spawning biomass. Thus by knowing the larval index for 1984 (1506 x 10^9), the spawning biomass (0.6 x 10^6 tons) for that year can be estimated.

Another example is provided in Figure 1.1. The sardine biomass was estimated from fishery data from 1940 to 1959 by the Murphy (1966) method. A larval index of abundance based on ichthyoplankton surveys was available from 1951 to 1969. The larval index was "calibrated" on the period of overlap (1951 to 1959) and it was then possible to make biomass estimates even though the fishery had essentially stopped.

3. Theoretical Considerations

Ideally, ichthyoplankton surveys conducted according to the methods presented in Section 2 would result in suitable estimates of the spawning biomass of any pelagic spawning fish. Unfortunately, even though the techniques may be standardized, the spawning behavior of pelagic organisms may vary widely enough to necessitate changes in techniques. For example, in individual cases it may be necessary to intensify the ichthyoplankton survey for a particular purpose or, conversely it may be possible to compromise some of the technical quality of the surveys and still obtain acceptable estimates of the spawning biomass. While the fundamental reason for this section is to provide information to determine individual requirements of standard ichthyoplankton surveys, it is hoped that this section will also serve two other purposes: 1) it should advise on ways in which surveys conducted with non-standard sampling techniques can be usefully related to the standard surveys; and 2) it should provide sufficient information on the sources and the magnitude of sampling error so that the survey specialist, with experience and the use of this manual and the research papers to which it refers, can make a contribution to the solution of continuing sampling problems.

3.1. Statistics

The present manual is not intended to be comprehensive with regard to statistical description and analysis of data. However, some subjects will be discussed to introduce the reader to particular problems encountered when sampling ichthyoplankton. Standard statistics texts should be consulted for the general concepts of statistical description, testing of hypotheses, and sampling design. For ichthyoplankton survey problems Southwood (1966) is recommended. A basic statistical description is given by Gulland (1966, 1969). Problems of biases and imprecision are treated in the UNESCO (1968) Monograph on Zooplankton Sampling. Sample design is treated specifically therein by Cassie (1968). The expense of marine plankton sampling and analysis may justify the services of a professional statistician for the planning of the data analysis.

3.1.1. Numbering Systems

The basic number system includes integers or whole numbers;

0, 1, 2, 3, 4, ... infinity (to an unlimited degree). These may also be extended to numbers on the negative side of zero to infinity. Between any two whole numbers there are fractions in this system which can be infinitely subdivided, e.g.:

0, 1, 2, 3, 4, ... infinity

2.1, 2.2, 2.3, 2.4,

2.21, 2.22, 2.23, 2.24.

Groups of numbers can also be elaborated to infinity as in the commonly referred to "orders of magnitude" system , e.g.:

0.1, 1, 10, 100, 1000, 10000, 100000, 1000000. . .

which in this example extends from one-tenth to one million by orders of magnitude. Since this system soon becomes unwieldy, an abbreviated system of "exponents" can be used:

$10^{-1} = 0.1$ $\quad$ $10^{3} = 1000$

$10^{0} = 1$ $\quad$ $10^{4} = 10000$

$10^{1} = 10$ $\quad$ $10^{5} = 100000$

$10^{2} = 100$ $\quad$ $10^{6} = 1000000$

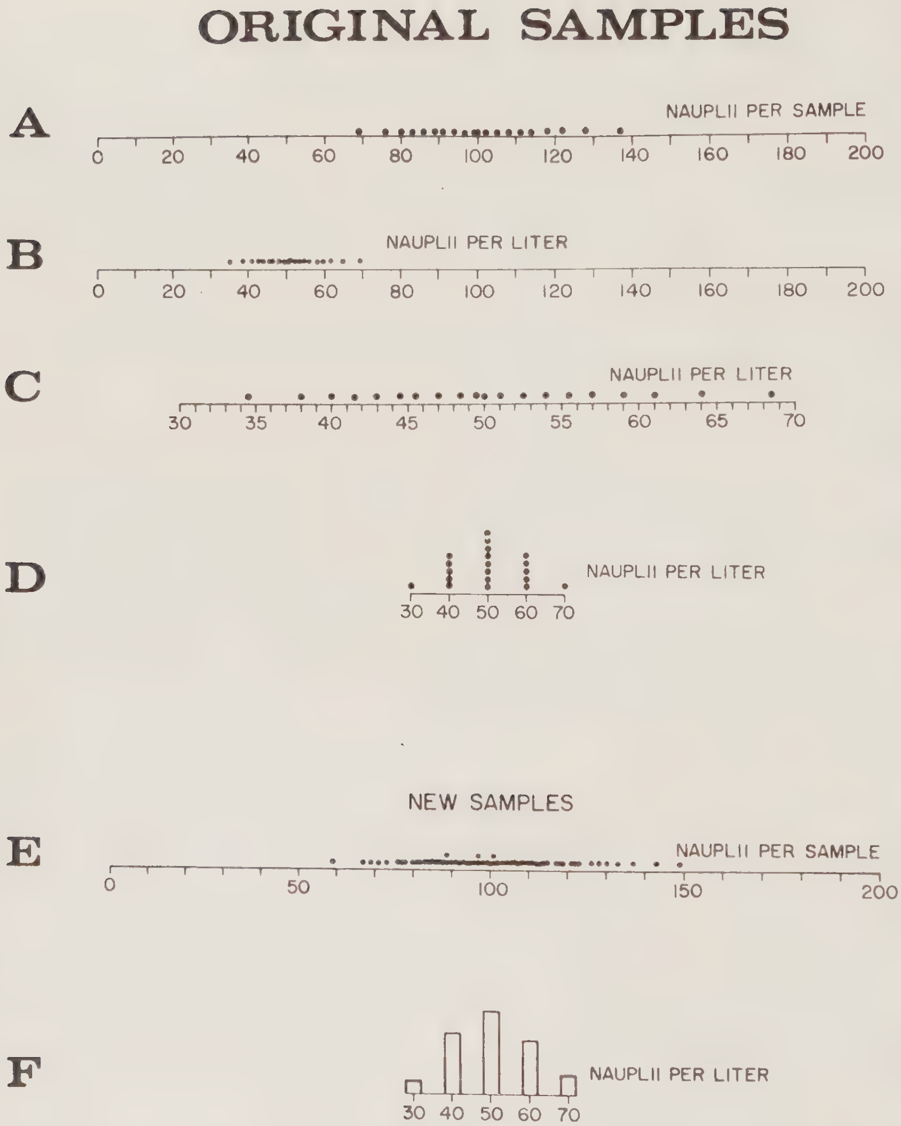


Figure 3.1. An example of sample data summaries. A) A graphic presentation of a number system from 0 to 200 with a dot at the position of each 2-liter sample count of nauplii. B) The 2-liter sample counts are represented as nauplii per liter. C) A segment of the scale has been expanded to the range of sample data expressed as nauplii per liter. D) The same sample array grouped in 10 nauplii per liter intervals, 30 (25-35), 40 (35-45), etc. E) New samples from the same population in nauplii per 2-liter sample. F) The sample array grouped in 10 nauplii per liter intervals. The length of each bar is proportional to the number of sample values within each interval.

These exponents can also be subdivided like fractions in the system of logarithms:

$10^{1.0} = 10$

$10^{1.1} - 12.6$

$10^{1.2} = 15.8$

$10^{1.3} = 20.0$

$10^{1.4} = 25.1$

$10^{1.5} = 31.6$

$10^{1.6} = 39.8$

$10^{1.7} = 50.1$

$10^{1.8} = 63.1$

$10^{1.9} = 79.4$

$10^{2.0} = 100.0$

$10^{2.7} = 501$ $10^{3.7} = 5012$

Approximations of logarithms of numbers and the number approximated by a logarithm may be found in books of mathematical tables. The precision of the approximation is controlled by the number of decimal places in the mantissa (the portion of the exponent following the decimal point). For example, the text table above may be used as one place table of anti-logarithms. The following is a two place table of logarithms, showing only the mantissae :

X	$\text{Log}_{10}X$	X	$\text{Log}_{10}X$
1	00	6	78
2	30	7	85
3	48	8	90
4	60	9	95
5	70		

The characteristic, or order of magnitude must be determined separately, as above. ($10^0 = 1$, $10^1 = 10$, $10^2 = 100$). The characteristic is the power of ten, and the mantissa is zero for all integer powers of ten. The mantissa is used for decimal fraction powers of ten. For example, $10^{0.70} = 5.012$, $10^{1.70} = 10 \times 5.012 = 50.12$, $10^{2.70} = 10^2 \times 5.012 = 501.2$, and $10^{3.70} = 10^3 \times 5.012 = 5012$. Note that the value X = 0 has no logarithm. Table 3.5 (below) is an abbreviated table of the mantissae. Tables of 4, 5 or 6 place logarithms and anti-logarithms are often available in books, and electronic calculators often have the capacity to generate 8 or 10 place equivalents.

3.1.1.1. Normal Distribution

Another form of number system is related to the distribution being sampled. For example, assume there is a well stirred brood tank of nauplii being reared to feed fish. Twenty successive two-liter samples are taken at random from the tank. Numbers (listed in descending order) of nauplii counted in each of the 20 samples are: 137, 128, 122, 118, 114, 111, 108, 105, 102, 100, 99, 97, 94, 91, 89, 86, 83, 80, 76, 69 (see also Fig. 3.1, line A). The ordered counts of nauplii per liter would be half the original numbers. On the fractional number scale they would be represented as in Fig. 3.1, line B. Only a portion of the fractional number system is necessary for this set of samples. On line C (Fig. 3.1), the samples are designated on a number scale which extends only from 30 to 70 nauplii per liter. Then all values are related to the nearest whole ten, 30, 40, 50, 60, 70, in line D (Fig. 3.1). Counts from 60 new samples of nauplii from the same tank are first represented by dots on the whole number scale (Fig. 3.1, line E) and then classified to "tens" in nauplii per liter (Fig. 3.1, line F).

There is a strong resemblance between the 20 samples and the 60 samples with regard to the central tendency of both distributions at 50 nauplii per liter and the absence of samples at 20 or less and 80 or more nauplii per liter. If the brood tank of nauplii had been completely separated into two liter units, there is reason to believe, on the basis of these two sets of samples, the general form of the distribution sample sizes in terms of nauplii per sample or nauplii per liter would be the same as the two sample sets illustrated. The only way to determine exactly how many nauplii were in the brood chamber would be to empty the chamber and count each nauplius: i.e., take a census. For many purposes the sample information was adequate and the census would contain little additional information. In many cases, like this, a census would be too expensive, unnecessary, or impossible. (For example, the census might kill the nauplii and render them unfit for fish food.) Also, during fast growth, the number of nauplii might change during a complete census but be stable for most purposes during a short sampling interval.

The example we have just examined was drawn from a "Normal" distribution. It was described by a set of samples which estimated two parameters; one for the position of the center on the number scale and one for the variation of the samples from this center. The central position is called the "arithmetic mean" or the "average" and the variation of the samples is called the "standard deviation." For the 20-sample series, the arithmetic mean (m) is determined by the equation:

$$m = \frac{X_1 + X_2 + X_3 + \dots + X_{20}}{20}$$

which reads, the arithmetic mean equals the sum of the first number plus the second number plus the third number plus all the numbers up to and including the 20th number which then is divided by 20. It is usually abbreviated using the Greek letter "Σ" (Sigma) for the "sum of" and the smaller letter "i" to denote the subscript number for each "x" in the following manner:

$$m = \frac{1}{20} \sum_{i=1}^{20} X_i$$

which for this set of data is:

$$m = \frac{1}{20} (2009)$$

$$= 50.2 \text{ nauplii per liter}$$

It is conventional to call this the sample mean "m" and to denote the population mean it is intended to estimate by the Greek letter "μ" (Mu). If the brood tank held 4000 liters, then 2000, 2-liter samples could be taken and the equation for the population mean would be:

$$\mu = \left(\frac{1}{2000}\right)\left(\frac{1}{2}\right)\sum_{i=1}^{2000} X_i$$

$$= 50 \text{ nauplii per liter}$$

The second parameter which describes the "Normal" population is called the standard deviation "s_x". It refers to each measurement (x_i) to the population mean (μ). The sum of the differences between each measure and the sample mean will be zero; thus the standard deviation is calculated from the square of the values of the deviations of individual measurements, or in conventional shorthand:

$$s_x = \sqrt{\frac{1}{n-1} \sum_{i=1}^{n} (X_i - m)^2}$$

where s_x is the sample estimate of standard deviation of the variable "x", "n" is the sample size, and "m" is the sample estimate of the population mean as above.

The value "n-1" is used as a divisor, because if "n" is used, the sample standard deviation tends to underestimate the population standard deviation. This tendency is corrected by the use of "n-1" or "degrees of freedom" as the divisor rather than "n", the number of observations. The value s_x^2 is called the sample estimate of the variance of "x".

In the "Normal" population, the "range" (lowest number to the highest number) is infinite in theory, and sample estimates of the range can only increase with increasing sample sizes. For this reason, it is usual to seek instead a pair of values which encompass a stated proportion (say 95%) of the population. The sample standard deviation defined above may be used to estimate pairs of values which will encompass any proportion of the population or sample distribution. Tables for this purpose are prepared for any situations which require great precision. Abbreviated tables for learning purposes are given in Tables 3.1 and 3.2 and these may suffice for all but the most demanding tests.

Table 3.1. Normal deviates (Z) and selected probabilities.

	.0	.1	.2	.3	.4	.5	.6	.7	.8	.9
0.	.500	.460	.421	.382	.345	.309	.274	.242	.212	.184
1.	.159	.136	.155	.097	.081	.067	.055	.045	.036	.029
2.	.023	.018	.014	.011	.008	.006	.005	.004	.003	.002
3.	.001									

Table 3.2 Areas under the normal curve.

	.0	.1	.2	.3	.4	.5	.6	.7	.8	.9
0.	.000	.040	.079	.118	.155	.192	.226	.258	.288	.316
1.	.341	.364	.385	.403	.419	.433	.445	.455	.464	.471
2.	.477	.482	.486	.489	.492	.494	.495	.497	.497	.498
3.	.499									

These tables (3.1 and 3.2) are complementary tabulations regarding the "normal" curve. The basic unit of the "normal" distribution is the difference between the observation and the population mean of all observations divided by the standard deviation. The unit is conventionally known by the letter "z" and calculated by the equation:

$$Z_i = \frac{X_i - \mu}{\sigma}$$

The letter "x_i" represents the variable under consideration, the Greek letter "μ" (Mu) represents the population mean as above, the Greek letter "σ" (Sigma) is the population standard deviation, and the letter "Z_i" is the number of standard deviation units "x_i" is from the population mean. In Table 3.1, the "Z" value of 0.0 represents the arithmetic mean of the distribution. The value at the intercept of the 0. row and the .0 column is .500 which is interpreted as meaning that half the sample values are above and half the sample values are below the arithmetic mean. The intercept of the 1. row and the .3 column is .097. This is read as 9.7% of all sample values are above the arithmetic mean plus 1.3 standard deviations and 9.7% of all sample values are below the arithmetic mean minus 1.3 standard deviations. In the complementary table 3.2, the intercept of the 1. row and the .3 column is .403. This is read that 40.3% of all sample values are between the arithmetic mean and the arithmetic mean plus 1.3 standard deviations and 40.3 % of all sample values are between the arithmetic mean and the arithmetic mean minus 1.3 standard deviations. Note that the values of the intercept of 1. row and the .3 column are .097 in Table 3.1 and .403 in table 3.2 and these values add to .500. All similar intercepts in the two tables are complementary thus either table alone would suffice for both types of expression. Lastly, asymmetric statements of probability may also be made from these tables. For example, the value at the intercept of row 1. and column .6 in table 3.2 is .445 and this may be stated: 44.5% of all sample values lie between the arithmetic mean and the arithmetic mean plus 1.6 standard deviations. Since we know that 50% of all sample values lie below the sample mean, this means 94.5% of all sample values lie below the arithmetic mean plus 1.6 standard deviations.

From the nauplii example (Table 3.3), the mean number of nauplii per liter is 50.225, the standard deviation is 8.91, the range, 34.5 to 68.5 nauplii per liter, and range of deviations extends from 15.725 nauplii per liter below the mean to 18.275 nauplii per liter above the mean. Expressed in standard deviation units the lowest value is 1.76 standard deviations below the mean and the highest value is 2,05 standard deviations above the mean. This is not an unreasonable asymmetry for such a small sample. One is justified for suspecting that these 20 samples have not explored the entire range of the 2000 samples possible from this tank. One sample standard deviation below the mean is 50.225 - 8.91 or 41.315. Sample values x_1, x_2 and x_3 are lower than this value. One sample standard deviation above the mean is 50.255 + 8.91 or 59.135. Similarly, sample values x_{18}, x_{19}, and x_{20} lie above this value. Thus, 3/20 or 15% of the values lie more than one standard deviation below the mean and 3/20 or 15% of the values lie more than one standard deviation above the mean. This means that 70% of all samples lie between the one standard deviation limits about the mean.

Table 3.1 at 1.0 z, gives the population value for this as .159 or 15.9% of sample values are more than one standard deviation above the mean and 15.9% are more than one standard deviation below the mean. This means that 100% - 15.9% or 68.2% are within ± one standard deviation unit of the mean. As stated above, Tables 3.1 and 3.2 are complementary in the sense that one gives the proportion of values likely to be outside set standard deviation units, while the other gives the proportion of values likely to be within given standard deviation unit boundaries. One should become completely familiar with both methods of presentation. Particular attention should be paid the value 1.96 standard deviations above and below the mean, because this means that 2.5% of all sample values lie outside the upper and lower bounds or 95% of the values lie within these bounds. This should be committed to memory for statistical work since estimation of the chance of being wrong only once in 20 times (95%) is a common statistical practice.

Thus, of the number systems mentioned so far, the whole number system, the fractional number system, the logarithmic system, and the normal system, the latter is the only system which is defined by a population of counts or measurements with the central position determined by the arithmetic mean and a number in "z" units of standard deviations above and below the arithmetic mean. One property of the normal system should be noted: the sample standard deviation is independent of the sample mean and thus the two parameters are independent measures of the population. It is important to realize that these constraints are not often satisfied in the natural distribution of animal populations in the sea or elsewhere, although on occasion parts of the sea may approach a state of being mixed somewhat like the tank of nauplii in the example.

Another example of the normal distribution and a simple graphic method for testing its utility, may be seen from the data of Fraser (1969) regarding the degree of penetration of oceanic plankton into the North Sea (Table3.4; Fig. 3.2.). For this example the North Sea extreme position of the oceanic plankton was recorded for 32 of the 45 years between 1920 and 1965. These positions were grouped into 30-mile categories in Table 3.4. At the right margin of the table the individual

Table 3.3. Ordered set of data from a normal distribution of samples of nauplii (an example).

SAMPLE	NAUPLII PER LITER	DEVIATION FROM MEAN
x_1	34.5	-15.725
x_2	38	-12.225
x_3	40	-10.225
x_4	41.5	-8.725
x_5	43	-7.225
x_6	44.5	-5.725
x_7	45.5	-4.725
x_8	47	-3.225
x_9	48.5	-1.725
x_{10}	49.5	-0.725
x_{11}	50	-0.225
x_{12}	51	+0.775
x_{13}	52.5	+2.275
x_{14}	54	+3.775
x_{15}	55.5	+5.275
x_{16}	57	+6.775
x_{17}	59	+8.775
x_{18}	61	+10.775
x_{19}	64	+13.775
x_{20}	68.5	+18.275
	$\sum x_i = 1004.05$	$\sum (x_i - m) = 0.0$
	$m = 50.225$	$md = 0.0$
		$\sum (x_i - m)^2 = 1509.2375$
		$s = 8.91$

Table 3.4. Penetration of oceanic plankton into the North Sea (after Fraser, 1969).

N°	n.mi.	YEAR									N	%	CUMULATIVE %
60.0	0	37									1	2.9	2.9
59.5	30												
59.0	60	32									1	2.9	5.7
58.5	90	51									1	2.9	8.6
58.0	120	26	59	60							3	8.6	17.1
57.5	150	20	23	24	25	30	35	36	57	63	9	25.7	42.9
57.0	180	21	33	48	50	58	61	62	65		8	22.9	65.7
56.5	210	28	52	53	55	56	64				6	17.1	82.9
56.0	240	38	39	49	54						4	11.4	94.3
55.5	270												
55.0	300	47									1	2.9	97.1
54.5	330												
54.0	360	46									1	2.9	100.0

group percentages and the cumulative group percentages are listed. Special graph paper, called probability paper, which has the cumulative percentage axis adjusted so that a "normal" distribution would be represented as a straight line, was then used. The axis is numbered from 0.01% to 99.99% The cumulative percentages from 17.1% to 97.1% from Table 3.4 were plotted in position (Fig. 3.2). The fact that these points are suitably close to a straight line is consistent with a hypothesis that the tendency of oceanic plankton to penetrate the North Sea is a "normally" distributed variable. The utility of this graphic method is that data sets can be simultaneously compared with respect to the "normality" of the distributions, the similarity of the means, and the standard deviations.

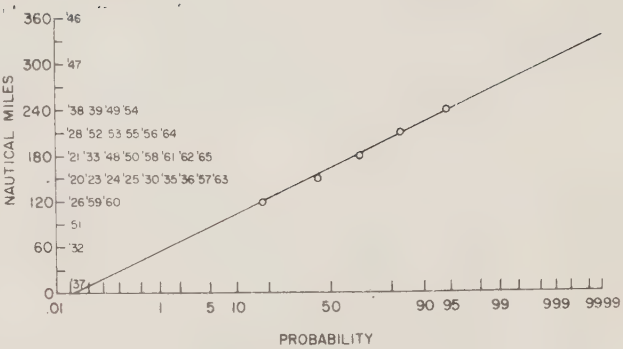


Figure 3.2. Penetration of oceanic plankton into the North Sea. The data in Table 3.4 have been plotted on normal probability paper by use of the cumulative percent frequency of Table 3.4 as the abscissa and the nautical miles of penetration recorded by planktologists as the ordinate. (After Fraser, 1969)

3.1.1.2. Lognormal Distribution

In the lognormal system (Aitchison and Brown, 1957), the sample values vary by a series of proportions of the central value rather than by a constant amount from the mean as in the Normal distribution. The uses of the central measure and the standard deviation are the same: the difference is that the equations are

$$\log g = \frac{\log X_1 + \log X_2 + \log X_3 + \ldots + \log X_n}{n}$$

or, as before

$$\log g = \frac{1}{n} \sum_{i=1}^{n} \log X_i$$

with the difference that the value "g" is the geometric mean of the set of numbers rather than the arithmetic mean (m) in the cases above. The sample standard deviation is similarly determined as above but now refers to a proportion to be multiplied or divided by the geometric mean to determine the distribution of values.

To save the trouble of calculating the geometric mean and the ratios of all values and the deviations of the ratios from unity, it is conventional to convert all values to logs (any base) and proceed as in the normal distribution. Table 3.5 provides a handy method for converting measurements or counts to logs. As stated above, if the numbers to be so transformed are between 1 and 10, the value in the table is used in a base 10 log transformation. If the numbers are between 10 and 100, the number in the table is preceded by the value "1.", and so on for other orders of magnitude. The conventional notation may also be used for the sample standard deviation of the log of the geometric mean:

$$s_{\log X} = \sqrt{\frac{1}{n-1} \sum_{i=1}^{n} (\log g - \log X_i)^2}$$

It is important to note two limitations on the use of the lognormal distribution: it must be demonstrated in each case (as in the normal distribution) that the variance is independent of the mean; and, "Lognormal theory cannot be applied directly to any sample which contains a zero value." (Aitchison and Brown, 1969, p. 94). For example, in the equation for the mean there is no logarithmic equivalent for x_i = '0':

Table 3.5. Three place mantissae for base ten logarithms.

	0	1	2	3	4	5	6	7	8	9
1	000	041	079	114	146	176	204	230	255	279
2	301	322	342	352	380	398	415	431	447	462
3	477	491	505	519	532	544	556	568	580	591
4	602	613	623	634	644	653	663	672	681	690
5	699	708	716	724	732	740	748	756	763	771
6	778	785	792	799	806	813	820	826	833	839
7	845	851	857	863	869	875	881	887	892	898
8	903	909	914	919	924	929	935	940	945	949
9	954	959	964	969	973	978	982	987	991	996

similarly in the equation for the standard deviation, the expression (log g - log x_i) is equivalent to division by '0' when x_i = '0'.

Users of this manual must assure themselves that in each case where lognormal analyses are used, sufficient care is taken that the assumptions critical to these analyses are examined. Bagenal (1955) lists several misuses of the lognormal distribution in marine plankton sampling and also describes the proper use of the method. In particular, the use of logarithmic transformations with the natural base "e" is recommended for sample statistics instead of the base '10' logarithm because of the ease with which unbiased arithmetic means may be derived from the mean and variance of ln x_i. The equation for the mean and variance are as above with the transformed variate.

3.1.1.3. Negative Binomial Distribution

In the Normal and lognormal distributions the variance is independent of the mean. In the negative binomial distribution, the variance is related to the mean in the following manner:

$$s^2 = m + \frac{m^2}{k}$$

A theoretical discussion of the properties of the negative binomial is beyond the scope of the manual (See Anscombe, 1949; Fisher, 1941). It has been found to be useful in the study of trawl catches of fish (Taylor, 1953).

One goal of statistical analysis, is to minimize the money and effort expended to obtain and interpret data. For the purpose stated for this manual, i.e., to monitor important changes in the spawning biomass of fish through ichthyoplankton surveys, one can identify the level of sampling effort necessary to achieve suitable separation of important differences. For example, if one wishes to distinguish between years differing by 25%, and if one assumes that the negative binomial is the most appropriate distribution model for ichthyoplankton, the following equation (Southwood, 1966, p. 20) will allow a first approximation of the number of samples needed to achieve the monitoring goal precision (25%):

$$N = \frac{\frac{1}{m} + \frac{1}{k}}{D^2}$$

"N" is the number of samples required, "m" is the sample mean of the number of eggs or larvae per unit area, "k" is the dispersion parameter of the negative binomial distribution, and "D" is the percentage level of difference required to discriminate between important and unimportant changes. For example, if we use the value for sardine eggs within one day of spawning (Smith, 1973) of about 100 eggs per 10 m^2 for "m", and a "k" of 0.014, and a "D" of 0.25 (25% difference) the number of samples required is:

$$N = \frac{\frac{1}{100} + \frac{1}{0.014}}{(.25)^2} = \frac{71.43}{0.0625} = 1143$$

The value of "D" is selected arbitrarily by the researcher to meet the goals of the program with respect to detection of important differences. The value of "k" may be estimated in various ways (Southwood, 1966) but the simplest estimator is:

$$k = \frac{m^2}{s^2 - m} \qquad k = \frac{10,000}{714,386-100}$$

As above, "m" is the arithmetic mean, and "s^2" is the variance or the square of the standard deviation "s". These sample values include the "0" samples, if any, in the preliminary samples.

Table 3.6. Estimations of the number of samples necessary to obtain certain levels of precision (D) for varying degrees of patchiness (k).

k	D			
	.05	.10	.25	.50
0.01	40004	10001	1600	400
0.02	20004	5001	800	200
0.05	8004	2001	320	80
0.10	4004	1001	160	40
0.20	2004	501	80	20
0.50	804	201	32	8
1.00	404	101	16	4
2.00	204	51	8	2

Table 3.6 represents a calculation of the number of samples required to discriminate between samples at levels of difference from 5% (0.05) to 50% (0.50) when the value of "k" varies from 0.01 to 2. The mean number of eggs or larvae per sample is arbitrarily fixed at 100 for this table.

3.1.2. Data Comparisons

In addition to the preparation of data summaries (see Section 2.3.) for practical evaluation of spawning biomass estimates, it is often necessary to examine certain statistical properties of the data set. For example, the incidence of a single large sample, during any single year of a 10-year sampling program, may lead one to believe quite falsely that the year has been unusual. It has been emphasized that the arithmetic mean is less and less efficient as the distribution of sample sizes gets skewed. Certain consequences of this fact may be lessened by understanding the distribution of spawning products (See Section 3.4. below) and presenting data in such a way as to expose rare large samples.

In Table 3.7 are three characteristic number distributions illustrating one "normal" distribution and two "lognormal" distributions with different degrees of standard deviation of the logs. All three distributions are centered at about 100, i.e., about an equal number of observations exceed 100 as are lower than 100. We will briefly examine some of the statistical properties of these three number sets.

Table 3.7. Three characteristic number distributions.

Normal		Log Normal "A"		Log Normal "B"	
149	99	479	96	17785	100
143	98	380	93	9813	89
137	97	339	91	5012	79
133	97	302	89	3981	71
130	96	269	85	2815	66
128	95	263	83	2239	63
126	94	246	81	1778	56
123	93	229	79	1413	50
122	92	214	76	1122	45
121	81	195	74	1097	40
119	90	191	72	891	35
118	89	178	69	708	32
117	89	166	63	631	28
115	88	162	62	562	25
114	87	159	58	501	22
113	86	148	56	447	20
112	85	145	55	398	18
111	84	141	52	355	14
110	83	138	51	316	13
109	82	135	50	282	11
108	81	132	47	269	10
107	80	129	45	251	9
106	78	123	43	224	8
105	77	120	41	200	6
104	76	118	39	178	4
103	73	115	37	159	4
102	71	110	32	148	3
101	69	107	28	141	2
101	67	105	20	126	1
100	59	102	15	112	0.7

	Normal	Lognormal "A"	Lognormal "B"
m (arithmetic mean)	100.55	123.70	899.70
s_x (standard deviation)	19.58	92.39	2642.71
Coefficient of variation	19%	75%	294%
ln g	1.99	1.99	2.01
s_g (standard deviation)	0.09	0.31	9.98
g (geometric mean)	98.67	96.70	102.21

In Table 3.8 we have divided the original normal number set into classes. In column "A", the class boundaries are 57.5 to 62.5, 62.5 to 67.5, and so on, for 19 classes. The representative value for each class, or "point" is 60, 65, 70, . . . 145. In Column "B" the class boundaries are 55 to 65, 65 to 75, and so on, for 10 classes, and the class points are 60, 70, 80, . . ., 150. In Column "C" the class boundaries are 50 to 70, 70 to 90, and so on for 5 classes. The point values are 60, 80, . . ., 140. In Column "D" the class boundaries are 40 to 60, 60 to 80, and so on for 6 classes. We find that the parameter estimates from these classified data sets differ very little from the population mean, 100.55, and the population standard deviation, 19.58. In each case, the "point" of the class was multiplied by the frequency value for the class, the results were summed and divided by the summed frequency. It is likely, the "C" or "D" classifications would be more easily understood as a normal frequency distribution, by inspection, than any of the other classified distributions or the complete data set itself (Table 3.7).

Table 3.8. Sample frequency distributions with varying class boundaries and points for the normal distribution in Table 3.7.

POINT	POINT ± 2.5	POINT ± 5	POINT ± 10	POINT ± 10	UNGROUPED
50					
55				1	
60	1	1	3		
65	1				
70	2	4		8	
75	3				
80	4	8	17		
85	5				
90	6	12		22	
95	6				
100	6	12	22		
105	5				
110	5	10		19	
115	4				
120	4	6	14		
125	2				
130	2	4		8	
135	2				
140	0	2	4		
145	1				
150	1	1		2	
m	100.58	100.50	99.67	100.33	100.55
s	19.79	19.43	20.00	20.99	19.58

In a similar manner, the logarithmic distributions may be summarized to inspect the frequency distribution. In Table 3.9 one may see the two lognormal number sets summarized by classes. The classes increase by multiples of four (any multiple may be used) and the class boundaries are 0.25 to 1, 1 to 4, 4 to 16, and so on for nine classes, and the class points are the geometric means of the class boundaries, 0.5, 2, 8, 32, 128, . . . , 3276. One must note that the arithmetic means are not particularly precise estimates of the population mean, but they are likely no more imprecise than sample estimates of 10 or 20 from distributions of this kind. Still the general lognormal appearance of the data is emphasized and the lognormal and arithmetic parameters of the mean and standard deviations are unbiased.

It is important to become familiar with the distributions for each planktonic stage for each species of fish. In this way, errors in judgment may be avoided or minimized.

Some examples from the CalCOFI program may serve to illustrate some kinds of statistical distributions of ichthyoplankton. For example, the fundamental sample distribution of sardine eggs has not changed markedly, even though the population

Table 3.9. Sample frequency distributions with even logarithmic class boundaries and log-normal frequencies (Table. 3.7)

CLASS BOUNDARY			LOG	LOG-NORMAL	LOG-NORMAL
LOWER	UPPER	MID-POINT	MID-POINT	A	B
.25	1	0.5	-0.30		1
1	4	2	0.30		3
4	16	8	0.90	1	9
16	64	32	1.51	17	12
64	256	128	2.11	36	14
256	1024	512	2.71	6	11
1024	4096	2048	3.31		7
4096	16384	8192	3.91		2
16384	65536	32768	4.52		1
			m	137.20	1189.57
			s	132.33	4425.54

has decreased 20-fold (Table 3.10). The scale of sample has been different with each decade, but the basic distribution of the all-important large samples remains proportionate. The lower end of the distribution is a sampling threshold and it appears to be essentially lognormal as in 1931-32 but the "unit" sample (one egg per sample) appears to be a pool of all areas less than the upper boundary of the smallest sample size class. Thus the high-speed sampler of 1950 with a small mouth opening, could only represent unit samples for all areas with an average of less than 256 eggs per 10 m^2. One may also note the remarkable stability of the standard deviation and the negative binomial "k".

The sensitivity of the sample frequency distribution is illustrated by the spawning cycle of the hake (Table 3.11) and the respective samples of eggs and larvae from a typical hake season, December 1954 through April, 1955. This is probably the most intense pattern exhibited by ichthyoplankton in the California Current. This will likely be explained by the fecundity of the individual females, the habit of spawning below the mixed layer of the ocean, and the long persistence of eggs and larvae in the colder waters.

One is often confronted with questions like "Are samples of type "A" comparable with samples of type "B"?" Of the statistical tests, few are as widely useful in ichthyoplankton sampling as the Kolmogorov-Smirnov Test (Tate and Clelland, 1957, p. 62). Two examples are provided here; one in which the samples are drawn from different distributions and one in which the samples are drawn from the same distribution.

The first example is drawn from a test which asks the question "Are anchovy eggs the same diameter in August of 1972 as they were in February of 1972?" In Table 3.12, the midpoints of the frequency classes of the diameters of the eggs are listed as fractions of a millimeter from 0.5643 to 0.8550 and the number of eggs measured at each size is in the second column. The next column lists the percent each category is of the total and the last column is the cumulative sum of the percents for the month of February.

Table 3.10. Sample frequency distributions of sardine egg samples at different levels of population taken with different plankton tows.

CLASS BOUNDARY ($N/10m^2$)			GEAR TYPE AND YEAR OF SAMPLES				
LOWER	UPPER	MID-POINT	CF&G 1931-32	1-Meter 1941	1/2-Meter 1941	High-Speed 1950	CalCOFI 1959
.0625	.25	.125	2				
.25	1	.5	4				
1	4	2	6	21			28
4	16	8	7	22	8		28
16	64	32	14	16	15		30
64	256	128	12	31	29	77	23
256	1024	512	13	27	14	20	12
1024	4096	2048	5	17	10	7	5
4096	16384	8192	2	3	2	1	4
		n	65	137	78	105	130
		m	544	569	ca.619	ca.406	410
		s	1466	1317	ca.1389	ca.900	1450
		k	0.136	0.187	0.196	0.207	0.080
		SPAWNING BIOMASS (Millions of Tons)	3.9	2.7	2.7	1.0	0.2

Table 3.11. An example of the sample frequency distribution of Pacific hake eggs and larvae by month (1954-55).

CLASS BOUNDARY		EGGS						LARVAE					
LOWER	UPPER	DEC	JAN	FEB	MAR	APR	TOTAL	DEC	JAN	FEB	MAR	APR	TOTAL
1	4	4	9	2	7	12	34	12	11	3	11	6	43
4	16	11	19	7	22	22	81	11	17	14	24	29	95
16	64	7	14	20	30	25	96	6	22	26	37	27	118
64	256	6	10	18	16	12	62		9	24	22	11	66
256	1024	0	12	12	7	3	34		7	12	7	7	33
1024	4096	1	7	9	6		23		1	9	0		10
4096	16384		4		2		6		1		1		2
16384	65536		2				2						
65536	262144		2				2						
	n	29	79	68	90	74	340	29	68	88	102	80	367
	m	108	4846	406	394	55	1333	10	233	325	157	76	182
	s	376	21169	669	1288	104	10364	12	1019	607	813	141	689
	k	.083	.052	.367	.094	.283	.017	.901	.052	.287	.037	.292	.070

Table 3.12. Worksheet for Kolmogorov-Smirnov test demonstrating the difference between anchovy egg diameters in February and August 1972.

DIAMETER (mm)	AUGUST			FEBRUARY			DIFF. (%)
	FREQUENCY	FREQUENCY (%)	CUMULATIVE FREQUENCY (%)	FREQUENCY	FREQUENCY (%)	CUMULATIVE FREQUENCY (%)	
.5643	3	.5	.5				.5
.5814	12	2.0	2.5				2.5
.5985	30	5.0	7.5				7.5
.6156	75	12.5	20.5				20.0
.6327	87	14.5	34.5				34.5
.6498	96	16.0	50.5	6	1.0	1.0	49.5
.6669	90	15.0	65.5	18	3.0	4.0	61.5
.6840	72	12.0	77.5	84	14.1	18.2	59.3
.7011	51	8.5	86.0	75	12.6	30.8	55.2
.7182	51	8.5	94.5	135	22.7	53.5	41.0
.7353	12	2.0	96.5	96	16.2	69.7	26.8
.7524	6	1.0	97.5	69	11.6	81.3	16.2
.7695	9	1.5	99.0	48	8.1	89.4	9.6
.7866	6	1.0	100.0	30	5.1	94.4	5.6
.8037				24	4.0	98.5	1.5
.8208				6	1.0	99.5	0.5
.8379							0.5
.8550				3	0.5	100.0	0.0
N	600			594			
m	.6614			.7285			
s	.0422			.0368			
$D_{.05}$							5.6%

Table 3.13. Cumulative frequency table for the Kolmogorov-Smirnov test demonstrating the similarity between measurements of a group of anchovy larvae by two people.

LENGTH (mm)	CUMULATIVE FREQUENCY (%)	CUMULATIVE FREQUENCY (%)	DIFFERENCE (%)
2.0	0.5	0.5	0.0
2.5			
3.0	1.6	1.6	0.0
3.5	2.7	5.9	3.2
4.0	14.4	16.2	1.8
4.5	19.8	20.0	0.2
5.0	28.9	35.7	6.8
5.5	36.9	42.2	5.3
6.0	46.0	49.2	3.2
6.5	51.9	53.0	1.1
7.0	59.9	61.6	1.7
7.5	67.4	70.8	3.4
8.0	73.8	76.2	2.4
8.5	78.6	79.5	0.9
9.0	87.7	88.1	0.4
9.5	91.4	90.8	0.6
10.0	94.1	95.1	1.0
10.5	96.8	96.2	0.6
11.0	98.4	97.8	0.6
11.5		98.4	0.0
12.0	98.9	98.9	0.0
12.5	99.5	99.5	0.0
13.0			
13.5			
14.0			
14.5			
15.0			
15.5		100.0	0.5
16.0	100.00		0.0
$D_{.05}$			7.2

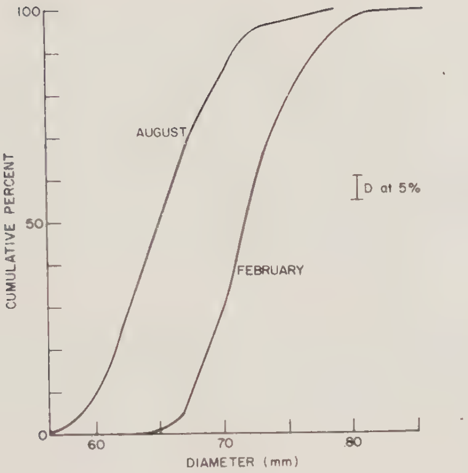


Figure 3.3. Illustration of the Kolmogorov-Smirnov comparison of sample frequency distributions of anchovy egg diameters from samples collected February and August of 1972. The difference (D), that is significant for the 5% level and 594 samples, is shown as a vertical line near the right margin.

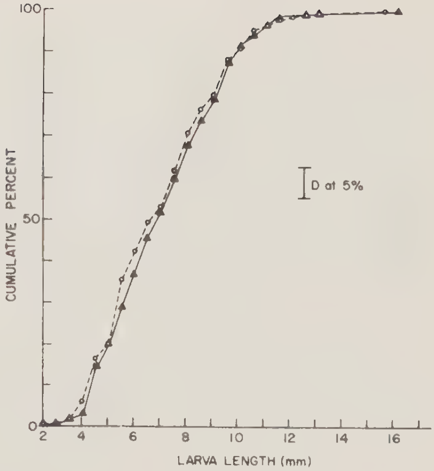


Figure 3.4. Illustration of the Kolmogorov-Smirnov comparison of sample frequency distributions of the lengths of anchovy larvae as measured by two people. The difference (D) that is significant for the 5% level and 356 samples is shown as a vertical line near the right margin.

The same columns are listed for the August samples. The final column is a difference column. For a 5% level of significance, the maximum difference is compared to:

$$D = \frac{136}{\sqrt{N}}$$

$$= \frac{136}{\sqrt{594}} = 5.6\%$$

where "D" is the significant difference level and N is the number of sample measurements (594 in this instance). The fact that the two curves differ by more than 5.6% is taken as conclusive that the difference is significant and that anchovy eggs were smaller in August of 1972 than in February of the same year. The two cumulative percent curves are plotted in Figure 3.3.

In example 2, the question is "do two plankton sorters derive the same length-frequency curve from a sample of 356 anchovy larvae?" In Table 3.13, only the category values and the cumulative frequencies and differences are listed. In this instance, significance at the 5% level is indicated by difference in cumulative percentages greater than 7.2% ($D = 136/\sqrt{356}$). Since no difference exceeding that value occurs, this may be interpreted as supporting the idea that the same 356 larvae were measured essentially the same by two independent plankton sorters. Figure 3.4 illustrates the two cumulative percentage curves for this example. The value "136" in this example is for a large number of samples (>100) to test a difference at the 5% level.

3.1.3. Advice on Data Transformations and Comparisons

It is the recommendation of the senior author that no transformation of data be done without the documented advice of a professional statistician. The widely used log transformation has no explicit or useful method for treating "0" observations. The "0" observations are necessary for determining the edge of the spawning area and are frequent within the spawning area. It is easy to misuse analyses based on log transformations (Bagenal, 1955) and analysis of variance and kindred tests can sense a significant difference in geometric mean when the arithmetic means are identical and detect no difference in geometric means when the arithmetic means are different. In some cases, the log transformation generates a set of values in which the variance is still a function of the mean, thus stabilization of variance is not a guarantee of transformation.

This manual is aimed at standardized conduct and reporting of fish egg and larval surveys, not analysis. In brief, we recommend a generalized distribution which 1) accommodates contagian or patchiness, 2) has explicit zero terms, 3) approximates a poisson at low mean values, and 4) does not assume independence of mean and variance. The negative binomial is our provisional recommendation for data analysis for data of the type collected in the CalCOFI surveys.

3.2. Volumetric Sampling

The earliest objective of quantitative plankton sampling was to take samples from the bottom to the surface under a defined unit of sea surface area. The earliest nets did not accept all the water encountered in the column, and factors for the correction of this bias were calculated by Hensen (1895) and Birge (1895). Reighard (1897) suggested the use of a flowmeter to record volume filtered. Kofoid (1897) pointed out that many smaller organisms were extruded through the meshes. Planktonic organisms were observed to avoid the net (Mackintosh, 1934). The survey procedures recommended in this manual (Section 2) do not eliminate these biases, but with care in equipment design and use, these biases and some of the technical sources of variability can be evaluated or minimized.

3.2.1. Volume and Distribution of Water Filtered

The estimation of spawning biomass requires quantitative samples of the planktonic spawning products expressed as numbers under a unit area of sea surface. This estimation can best be obtained from a tow designed to filter at a constant rate per unit depth from below the deepest occurring egg or larva to the surface. On the continental shelf, and in bays and lakes where quantitative sampling began, the vertical tow was the method of choice. This manual recommends an oblique tow instead because the vertical tow cannot be conducted with precision on the high seas.

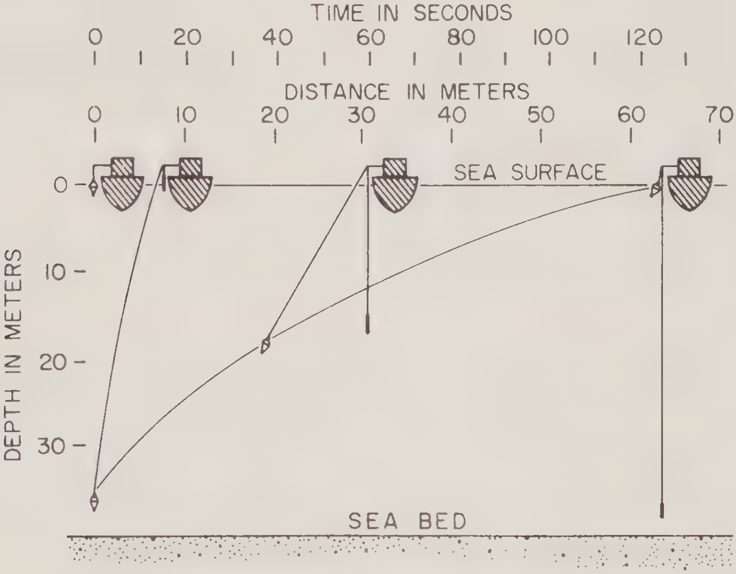


Figure 3.5. An example of the path of a Hensen net when fished vertically with the ship adrift. (From A.C. Simpson, 1959).

A.C. Simpson (1959) drew attention to the fact that "vertical" hauls from a drifting ship (Figure 3.5) filtered more water than planned, and he accordingly furnished correction factors for different rates of drifting. Unfortunately, a second bias occurs in stratified waters which cannot be easily corrected. In a vertical tow the assumption is that an evenly integrated tow has been taken from the maximum depth to the surface. It is quite clear that this assumption is systematically violated in vertical tows from drifting ships or from static ships with underlying current stratification. The effect is that the rate of ascent is rapid in the deep portion of the tow, and more and more water is filtered from each unit depth as the surface is approached (Smith, Counts and Clutter, 1968) leading to an unrepresentative sample of the water column biased in favor of the superficial waters.

This effect will not be serious in well mixed waters.

Swells and the rolling of the ship also cause the vertical tow net to pump portions of its sample back into the sea. The same motions of the ship cause the vertical sample to be accelerated so that portions of the sample lying on the mesh are likely to be extruded through the apertures.

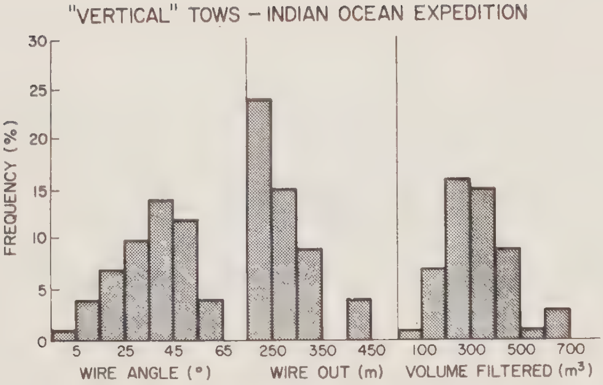


Figure 3.6. A sample of the wire angles, wire out to reach 200 meters depth, and the volume of water filtered during each tow using the Indian Ocean Standard net. (After Motoda, Konno, Kawamura and Osawa, 1963).

Some examples of the poor quality control of vertical tows are available from recent expeditions. For example, during the Indian Ocean Expedition (Motoda, Konno, Kawamura, and Osawa, 1963), a 1.13 m diameter ($1 m^2$ in cross section) net was towed "vertically". Figure 3.6 illustrates the variability in the wire angle, the amount of wire required to reach 200 meters, and the volume of water filtered for these tows. Table 3.14 lists some of the variations in the wire angle of vertical tows made during the Cooperative Study of the Kuroshio (CSK). Here, too, instead of the intended vertical tow, the average tow had a 25° wire angle, the standard deviation(± 2 s.d.) of the average tangent was 0.31, and the actual range of angles was from 9° to 65°. Also, the extended forward disturbances caused by the tow wire augment the usual avoidance problem (Clutter and Anraku, 1968).

Two major faults of the Hensen net are the towing bridle and towing cable ahead of the net (see Section 3.3.2. below) and the inability to locate a stable flow area in which to place a flowmeter (Figure 3.7). The reduction cone causes acceleration of the water near the periphery of the mouth because of the reduced pressure

Table 3.14. Recorded angles of tow for "vertical" tows in the Cooperative Study of the Kuroshio (CSK).

ANGLES OF STRAY	FREQUENCY
0°	16
5	35
10	58
15	52
20	59
25	33
30	59
35	37
40	38
45	11
50	11
55	3
60	0
65	2

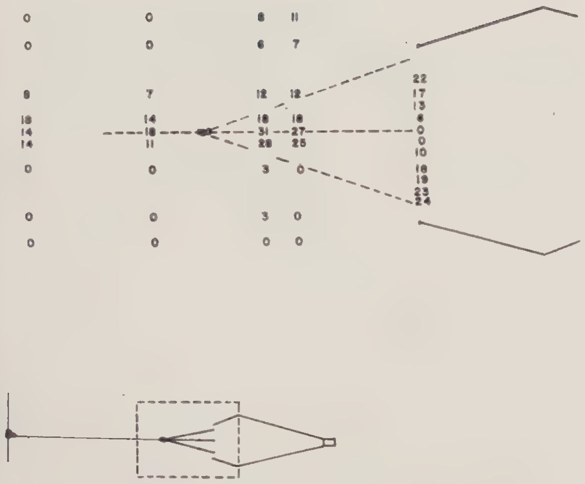


Figure 3.7. A comparison of the accelerations of water in the mouth and several transects ahead of the Hensen net. The numbers represent the difference between the channel flow with and without the net present in cm/sec. The inset illustrates the entire towing arrangement in the test channel.

behind the cone. This effect diminishes toward the center of the net behind the bridle apex. If the towing speed could be made suitably constant, the flow could be calculated, but the degree of acceleration is quite sensitive and dependent on tow speed, therefore the variations experienced in high-seas towing would preclude the collection of precise and accurate filtration performance data.

3.2.1.1. The Oblique Tow

The progress of the oblique tow is actively regulated by the ship when it is underway. In areas where currents are relatively slow, such as the California Current region, it has been found possible to fish plankton nets from the standard 210m depth with reasonable consistency [e.g., 206m ± 16m (2 s.d.)]. In areas with strong undercurrents, such as the Eastern tropical Pacific (Ahlstrom, 1971, 1972) less consistency is achieved (e.g., 203m ± 37m) although the variation is still within acceptable limits. One important factor to consider when comparing oblique tows with vertical tows is that the greatest errors in the oblique tows occur at depth and the error diminishes toward the surface (Figure 3.8). The vertical tow path error is cumulative toward the surface. Variation in the volume filtered in a series of oblique tows is usually much less (e.g., volume filtered = $649m^3$ + $86m^3$ for 165 tows of the CalCOFI net) than it is in vertical tows (e.g., the Indian Ocean Standard net, Fig. 3.6).

The tow-by-tow variation in these properties can be measured adequately from the surface by monitoring the wire angle closely. Fig. 3.9 demonstrates this by showing the similarity of tow paths for an ideal tow as determined from wire angle readings and a bathykymograph. About the best that can actually be accomplished in maintaining a straight oblique tow path on a net tow under ideal conditions is illustrated in Figure 3.10. Part "a" of that figure shows the ideal tow path, the tow path estimated by a bathykymograph (part "b"), and the time course of the rate of ascent. In the ideal standard tow, 20 meters of wire are retrieved per minute with a wire angle of 45°. The ideal rate of ascent is 14 meters per minute. In the tow in question (Fig. 3.10), the rate of ascent varied ± 30% from the ideal rate. An example of the maximum acceptable variation from the ideal tow path, for the purposes of standardization, is illustrated in Figure 3.11. In this example the rate of ascent varied ± 84% from the ideal. Where the rate of ascent is higher than average, less water is filtered per unit depth. The variation in tow path can be evaluated by converting the wire angle readings, which are made at 30 second intervals during the tow, to tangents and calculating the average tangent and standard deviation for the tow (Table 3.15). Standards can be established ahead of time for accepting or repeating tows. If the standard deviation of the average tangent is too great (e.g., 2 s.d. ≥ 0.1) the tow should probably be repeated. One way to assure a good tow is to maintain the wire between 42° and 48° (45° ± 3°). The constancy that is possible is exemplified by a series of 204 high-seas tows made in a temperate area. The average tangent was 1.077 (± 2 s.d. = 0.084) with 95% fiducial limits of 0.91 - 1.24.

The importance of the variation in the rate of ascent is underscored by the stratified nature of the oceanic environment. One of the earlier explanations for "patchiness" was the allegation of uneven ascent of the net through stratified layers of sardine eggs (Sette and Ahlstrom, 1948). This feature was also used to explain the fact that the use of volume filtration data was not significant in the analysis of variance of egg counts. The uneven passage of the net through the water column should be carefully avoided. Further effects of this uneven rate of ascent include the increased extrusion of flexible organisms during the faster part of this retrieval, and the possibility of the flowmeter stopping during the slower part of the fluctuation in rate of ascent.

3.2.1.2. Clogging

At times, material in the seawater may clog the mesh of the net thus lowering the filtering capacity of the netting. As long as the flowmeter continues to function, this deficit in water filtered will be monitored. As can be seen from Fig. 3.13 however, the sample taken gets progressively less representative with time. The tendency is to undersample the surface layer if clogging proceeds throughout the tow. In Figure 3.12 the trail of dye streaks through the netting indicates that clogging occurs evenly over the entire net surface, not just near the cod end. The rapidity with which clogging can occur is illustrated in Fig. 3.13. If clogging is routinely encountered, the only solution is to increase the filtering area (Smith, Counts and Clutter, 1968; Tranter and Smith, 1968) by adding extra panels of mesh in the cylindrical part of the net.

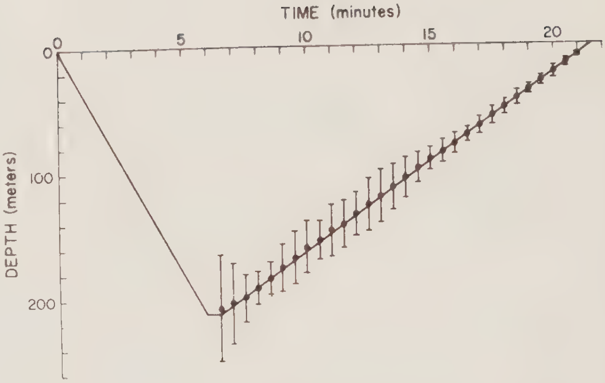


Figure 3.8. The ideal tow path in the CalCOFI oblique tow to 210 meters (solid line) and the average depth at each 10 meters recovered ± 2 standard deviations in a test series of 14 tows.

3.2.2. Avoidance

The use of ichthyoplankton surveys to monitor spawning biomass requires constancy of larval size distribution in the samples obtained. The size distribution of larvae captured in plankton nets is affected by two factors. In particular, as larvae grow they appear to undergo heavy mortality while at the same time they improve their ability to evade plankton nets. Understanding the relative importance of mortality and avoidance in the declining catch of fish larvae with increase in size should aid in the interpretation and understanding of the role of larvae mortality and recruitment of future stocks.

Research on avoidance was extensively reviewed by Clutter and Anraku (1968). Further work on an "ultimate" sampler by Murphy and Clutter (1972) points out the extreme nature of larval avoidance (Figure 3.14) and further explains why the search for an "ideal" sampler has not been very productive. It appears likely that the day-night difference in avoidance is only a small part of the total avoidance problem, the bulk of the avoidance being performed as well in the dark as in the light. Barkley (1964; 1972) described the relative capacities of larvae to avoid when given advance warning of the approach of the sampler. He indicated that the response starts three to four mouth diameters ahead of the net. Larger and faster tow nets may alter the ability of larvae to avoid very little because they intensify the disturbance and project it further ahead of the net.

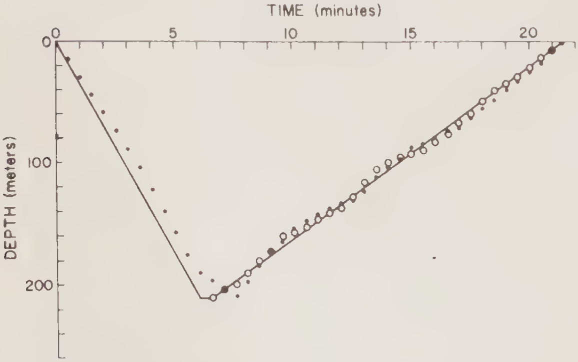
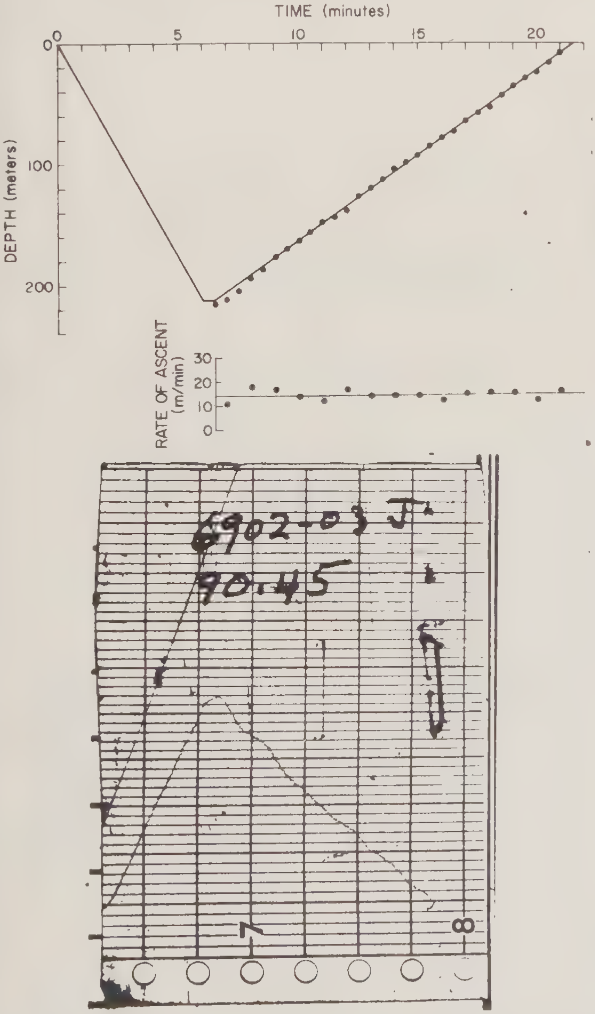


Figure 3.9. The ideal tow path of the CalCOFI net (solid line), the depth measured by bathykymograph (solid dots) and the depth estimated by the angle of stray and the wire out (open circles).

Figure 3.10. An ideal tow. a) In the upper figure the ideal tow path is illustrated (solid line) and the attained depths, determined by a bathykymograph, are solid dots. The first difference in the meter's depth each minute is illustrated in the lower portion of the drawing. This is the critical measure of the volume of water filtered for each unit depth. b) A bathykymograph trace of the same tow.



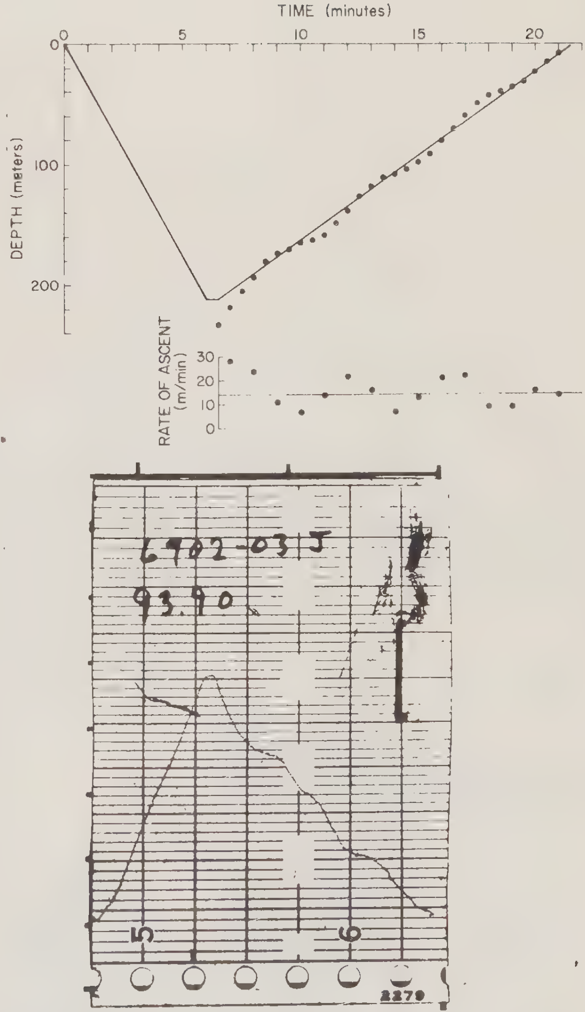


Figure 3.11. An extremely variable tow. a) In the upper figure the ideal tow path is illustrated (solid line) and the attained depths, determined by a bathykymograph, are solid dots. The first difference in the meter's depth each minute is illustrated in the lower portion of the drawing. This is the critical measure of the volume of water filtered for each unit depth. b) A bathykymograph trace of the same tow.

Table 3.15. An estimation of the variation in towing path derived from the average tangent and standard deviation of the tangents.

θ	tan θ	f
50°	1.1918	1
49	1.1504	2
48	1.1106	8
47	1.0724	8
46	1.0355	7
45	1.0000	4
$\bar{T}$	1.0735 (=47°)	
S_T	0.0486	
95% Fiducial Limits	.9782 - 1.1688 (= 44°-49°)	

Some mechanical cues for avoidance are available both day and night. Smith and Clutter (1965), Mahnken and Jossi (1967), and Tranter and Smith (1968) described the accelerations of water in front of the plankton net caused by the legs of the towing bridle, the towing bridle apex, and the towing cable. A simulation of a thoroughly clogged net (Fig. 3.15) illustrates the fact that the advanced warning due to a "bow-wave" effect is probably limited to the region of approximately one mouth diameter ahead of the net. The bridles without a net propagate measurable disturbances (Fig. 3.16) along the towing line as far as it proceeds ahead of the net, and particularly strong disturbances occur at the bridle apex. This is an important consideration in vertically towed nets. The absence of these disturbances is one of the most important features of the recommended Bongo nets.

The main reason for understanding day-night differences is to be able to correct sample data for size and time-of-day in order to make all the data obtained comparable for use in estimating spawning biomass. Lenarz (1973) found that the decreased catch per unit larval length for a set of CalCOFI tows increased in the order sardine, anchovy, hake and jack mackerel. To transform the data to a comparable basis regardless of day or night, or larval size, he fitted the equation:

$$\ln (N_{sd}/N_{s_0d}) = \ln A - B\,(s - s_0) + C_d(s - s_0) + \ln (E_{sd})$$

"N_{sd}" is the number of larvae of size "s" caught during time period "d", and "s" takes values s_0 s_1, $s_2 \ldots s_t$ where "s_0" is the modal size group and "s_t" is the largest size larvae with significant catch;"d" is the time of day, i.e., day (-1), or night (0)*, A is a constant, B is

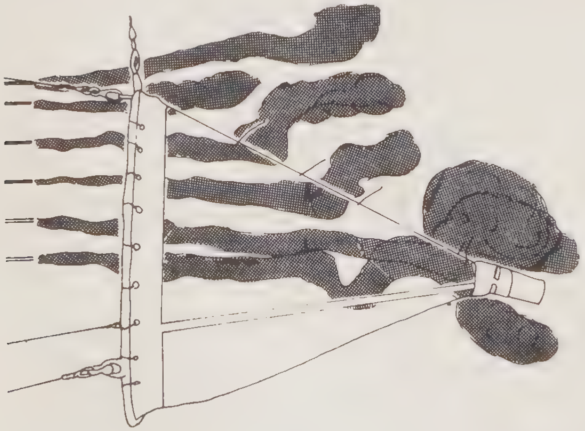


Figure 3.12. A composite drawing made from photographs of dye passing through an experimental net in a towing chamber. The yarn tabs perpendicular to the filtering surface are a separate indicator of flow.

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*This variable was incorrectly identified as day (0), night (1) by Lenarz (1973).

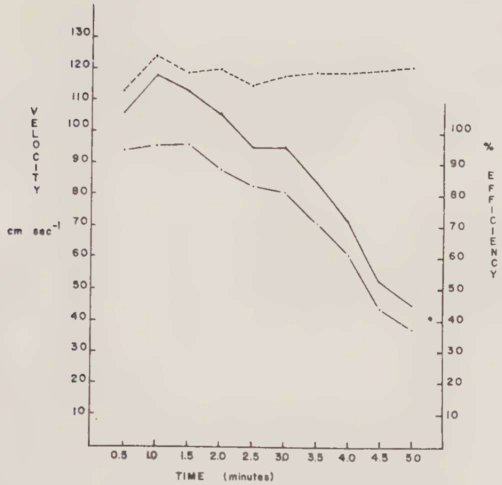


Figure 3.13. The clogging of a WP-2 (working party 2) 0.202 mm mesh conical net (UNESCO, 1968) under tow in Southern California nearshore water.

----- towing speed indicated by a telemetering flowmeter outside the net.

______ rate of flow through the mouth of the net indicated by a telemetering flowmeter inside the mouth of the net.

•___• ratio of the inside and outside readings times 100 (% efficiency)

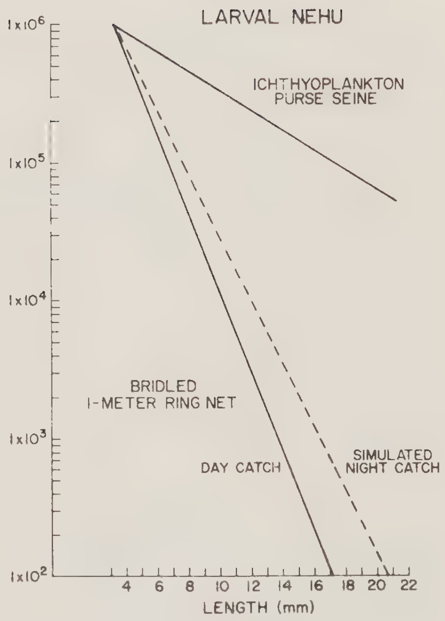


Figure 3.14. An example of the degree of avoidance of larvae (in this case larval nehu, Stolephorus purpureus) by day from a bridled ring net as compared to a plankton purse seine. (From Murphy and Clutter, 1972)

the instantaneous rate of decline in catch with size, "C" is the instantaneous rate of increase of the night to day ratio with size, and "E_{sd}" is the error term assumed to be independent of "s" and "d" and to have a log normal distribution.

The solutions to this equation were:

Species	B	C
Sardine	0.22	0.20
Anchovy	0.42	0.16
Hake	0.48	0.21
Jack Mackerel	1.18	-0.11

If the negative value of "C" for jack mackerel were significant it would mean that there is an increased tendency to be caught at a higher rate during daylight than during night. The smallness of the coefficient probably does not warrant such a conclusion and an alternate explanation is that jack mackerel of all sizes avoid the net as well at night as during the day.

3.2.3. Mesh Retention

The retention of small larvae is as important to the effective calculation of spawning biomass as the capture of larger larvae and juveniles is to prediction of recruitment. Probably more than half the anchovy larvae in the ocean, for example, are less than 4.25 mm long and extremely vulnerable to changes in filtration

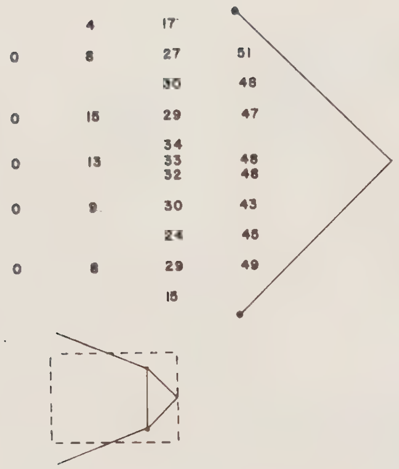


Figure 3.15. A one meter diameter solid cone suspended in a towing channel. The transects of figures represent the difference in channel velocity at those locations with and without the net and are expressed in cm/sec. (From Tranter and Smith, 1968).

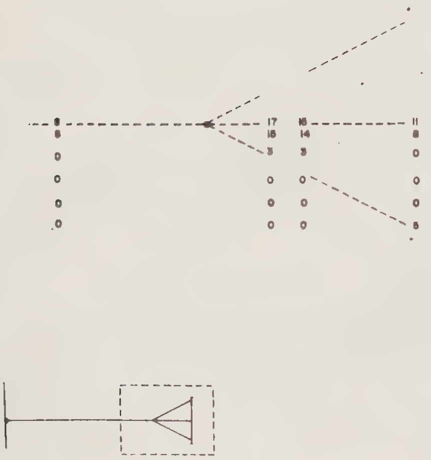


Figure 3.16. An illustration of the accelerations ahead of the towing apparatus of a net when no net is present. (From Tranter and Smith, 1972).

pressure and escapement and extrusion through the meshes. Lenarz (1972) estimated the retention ratio of anchovy and sardine in nets towed at constant speed and found the relationships:

$$s = a + bL$$

Where s is the mesh retention ratio of larvae of size "L" (less than 5.75 mm SL), L is the length of larvae, "a" is the usual intercept of a linear regression, and "b" is the slope.

For the silk CalCOFI net, the relationships were:

	a	b
Sardine	-.2382	0.2107
Anchovy	-.1942	0.1945

and the retention ratio by length was:

Length (mm SL)	Anchovy	Sardine
2.50	0.292	0.289
3.75	0.535	0.552
4.75	0.730	0.763
5.75	0.924	0.973

The static and dynamic relationships of mesh retention can be discussed. In Fig. 3.17 the width and diagonal measurements of four different mesh sizes are compared for their retention capabilities of anchovy and hake larvae. It can be seen that larvae are captured because of their length but they are retained because of their body depth which becomes a critical dimension. Another factor to consider is the variability in mesh size within the netting. For example this variability is greater in silk mesh nets than in those made of nylon (Fig. 3.18). Mesh variability is reviewed by Heron (1968). A good review of factors involved with mesh selection is given by Vannucci (1968).

In nets with high filtering rates, the complexities of extrusion and larval damage are encountered. These rates are functions of the square of the velocity and the ratio of mesh surface area to mouth diameter (Tranter and Smith, 1968). As yet, no generalizations can be made on the relationship between larval size, mesh size, towing speed and variance in towing speed. Until this analysis is completed, low constant towing speeds (1.5-2.0 knots) should be maintained. This is the primary consideration behind the recommendation of the "slow" Bongo nets.

An example of the severity of extrusion with increased towing speed can be seen in these preliminary data on percent

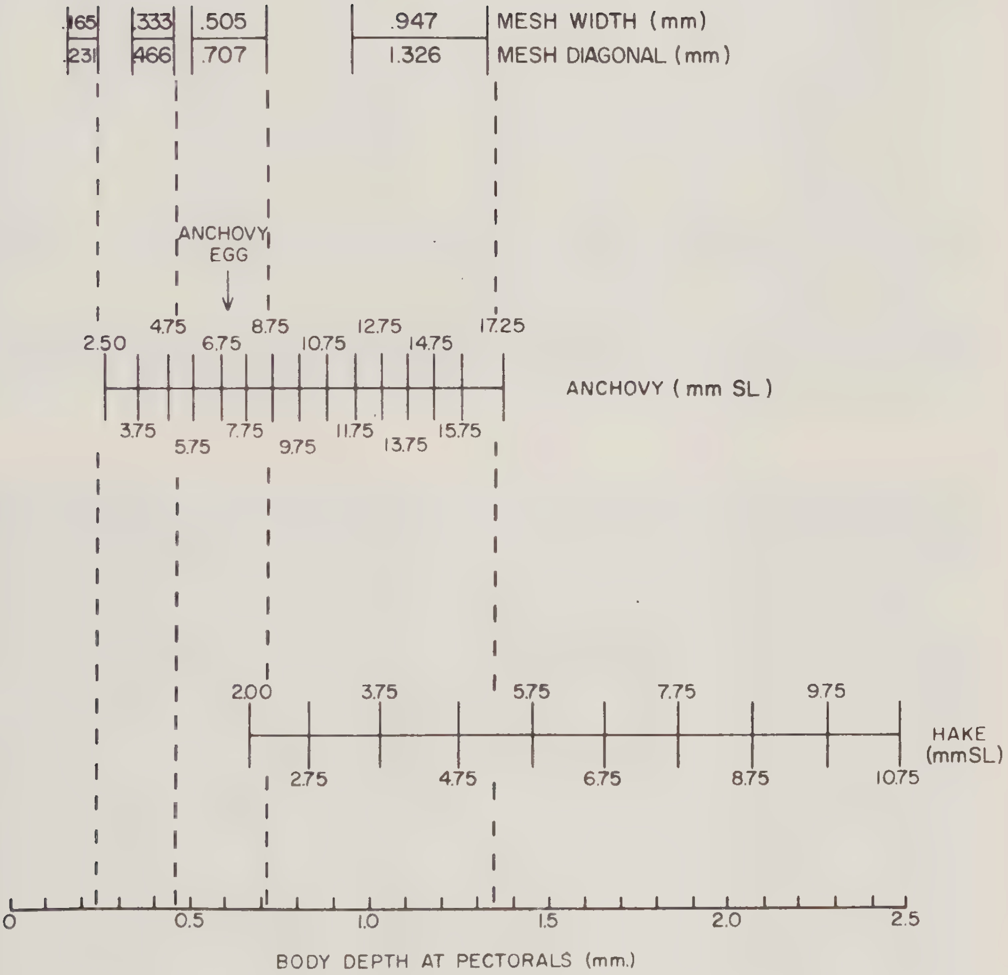
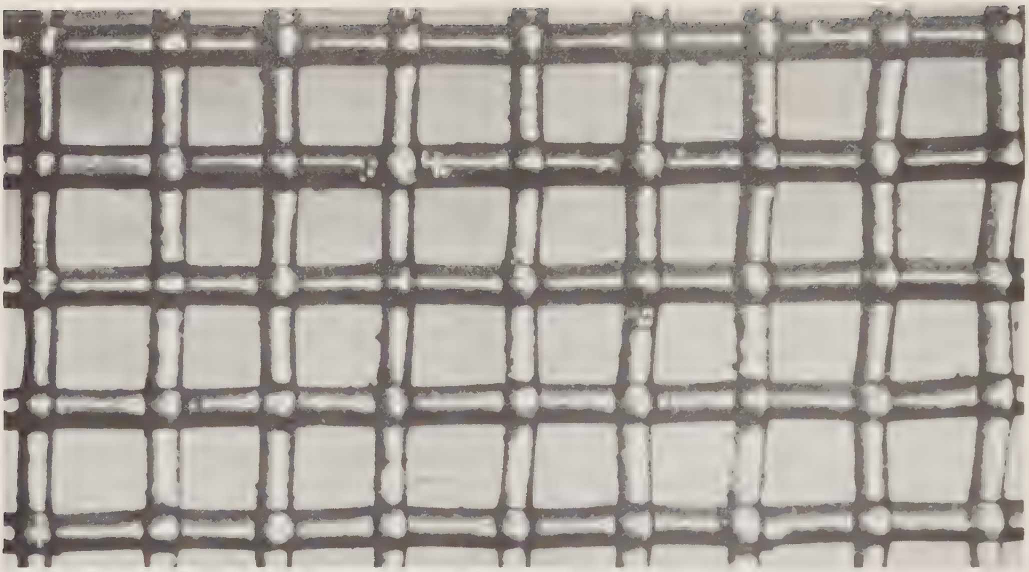

.165
.231
.333
.466
.505
.707
.947
1.326
MESH WIDTH (mm)
MESH DIAGONAL (mm)
ANCHOVY EGG
2.50
3.75
4.75
5.75
6.75
7.75
8.75
9.75
10.75
11.75
12.75
13.75
14.75
15.75
17.25
ANCHOVY (mm SL)
2.00
2.75
3.75
4.75
5.75
6.75
7.75
8.75
9.75
10.75
HAKE (mmSL)
0
0.5
1.0
1.5
2.0
2.5
BODY DEPTH AT PECTORALS (mm.)

Figure 3.17. An example of retention characteristics of various mesh sizes. The mesh width (left bar on upper line) and diagonal (right bar on upper line) are compared with standard length and corresponding body depth of anchovy and hake. The dashed line corresponds to the level of absolute retention. (Modified from Smith, 1972*)

*Smith, P.E. 1972. Extrusion. MARMAP, Technical Memorandum #6, June 7, 1972. Unpublished manuscript.



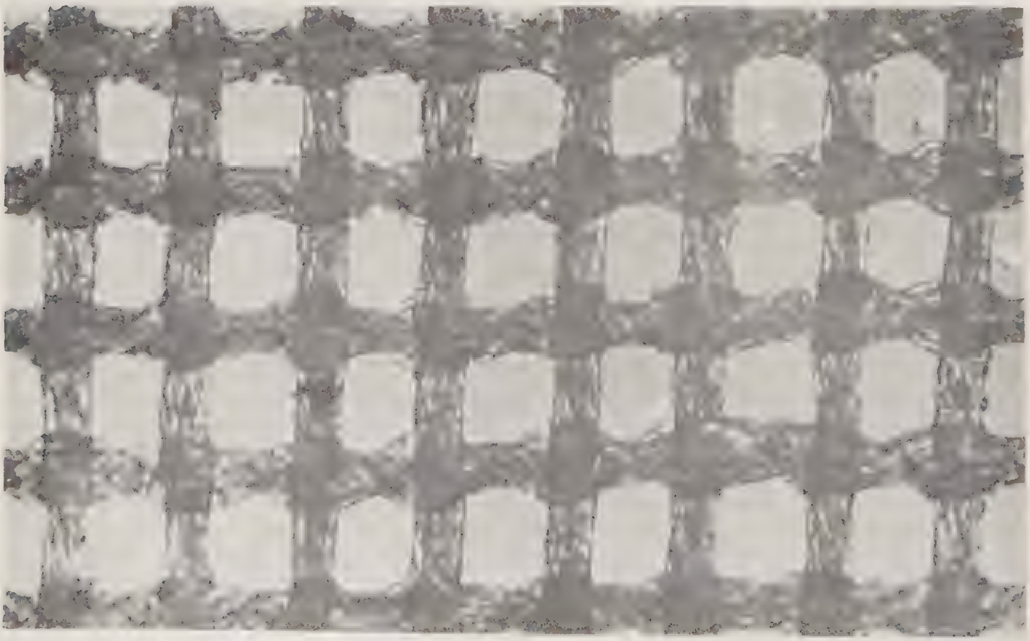


Figure 3.18. Above, 0.505 mm monofilament mesh (.505 Nitex*). Below, 0.55 mm mesh silk mesh [30xxx (extra heavy) GG (grit. gauze)].

of anchovy larvae retained from Smith (1972)* [based on ideas set forth by Saville (1959) and Heron (1968)]:

Anchovy Standard Length (mm)	Towing Speed (Knots)			
	1.5 **	2.00	3.15	4.14
2.50	.292	.478	.154	.063
3.75	.535	.565	.474	.137
4.75	.730	.777	.807	.285
5.75	.924	1	.802	.329
6.75	1	1	.752	.423
7.75	1	1	1	.826

3.2.4. Uneven Tow Trajectories

Current towing methods do not permit an analysis of the assumption that equal volumes of water are filtered at each depth. While these differences can be measured, and the effect on a given vertical distribution estimated, each tow in a survey must either be accepted or rejected, for no "standardization" or "adjustment" is tractable. Until directed research is completed on this problem, one can only say that a potential problem exists and that its magnitude is less than the variance associated with the normal level of patchiness encountered.

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* Smith, P.E. 1972, Extrusion, MARMAP Technical Memorandum #3, May 22, 1972. Unpublished Manuscript.
Smith, P.E. 1972, Extrusion, MARMAP Technical Memorandum #6, June 7, 1972. Unpublished Manuscript.

**CalCOFI silk/0.55 mm mesh (Lenarz, 1972); all others Bongo Nitex/0.505 mm mesh.

3.3. Sampling to Determine Spawning Area and Time

The geographic, vertical, and seasonal boundaries of spawning must be well defined for the analysis of spawning biomass. Since the primary costs of ichthyoplankton surveys are related to distance traveled by ship, understanding these boundaries may permit substantial reduction of sampling effort between the exploratory phase and the monitoring phase of the survey program. Also, the spawning products diffuse with time and are transported off the spawning grounds, and migrations of adults may occur during spawning. Both of these factors may affect the seasonal placement of boundaries.

3.3.1. Geographic Distribution

The pelagic habitat appears to permit spawning over vast areas. For example, the northern anchovy of the California Current regularly spawns over an area of 50 to 100 thousand square miles. The Pacific saury spawns so widely, beyond the usual boundaries of the CalCOFI survey grid, that a satisfactory westerly boundary has never been usefully defined (Figure 3.19) and it is possible that the distribution is trans-Pacific. In this figure, the incidence of saury occurrence has been plotted at stations sporadically occupied around the periphery of the usual CalCOFI area. Were it to become necessary, these peripheral stations could be used to design a survey to surround the spawning area of this species. The basic ability to define the geographic boundaries of spawning is one criterion for deciding whether the ichthyoplankton survey technique is feasible for a particular fish species.

Figure 3.20 shows the spawning of jack mackerel (Trachurus symmetricus) was undoubtedly occurring to an important extent outside the usually surveyed area but the north-south and the seasonal distributions appeared to be adequately enclosed. In some instances such as these, a conservative estimate of spawning biomass may be made (Ahlstrom, 1968; Gulland, 1970) and plans may be modified to enclose the spawning in subsequent surveys. In this way the monitoring surveys for sardine and anchovy may be used as the exploratory surveys of other species with only small technical costs added to the major goal of the survey.

Colebrook (1973) has examined alternative strategies in sampling simulated seasonal and geographic patterns. His model demonstrated that under the conditions simulated there is little difference among random, stratified random, grid, and route transects over a region at several degrees of pattern intensity. However, the grid was clearly more expensive than the others in terms of the travel distance to occupy stations. Colebrook (1973) also emphasized that the evenly spaced grid in time and space has advantages for mutifactorial treatment of data. It should also be kept in mind that many oceanographic techniques require a station transect normal to the coast, and great economies are available for combined fisheries, biological and oceanographic surveys, since ship-time is the greatest unit cost of each type of survey.

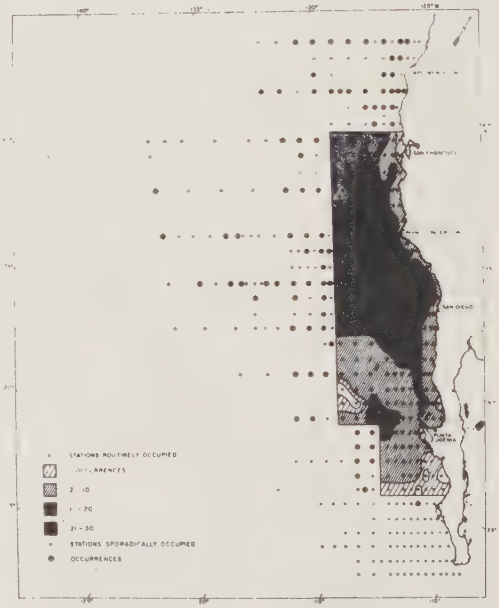

Figure 3.19. A composite drawing showing the incidence of saury eggs in the usual CalCOFI survey area and around the periphery. (From Smith, Ahlstrom, and Casey, 1970)

Switzer (1967) has examined the loss of precision resulting from the change from an even grid to a grid which concentrates stations along lines and separates the lines by an equivalent proportion. For example, the error level from a square grid increases only 10% when a 2:1 rectangular grid is used and

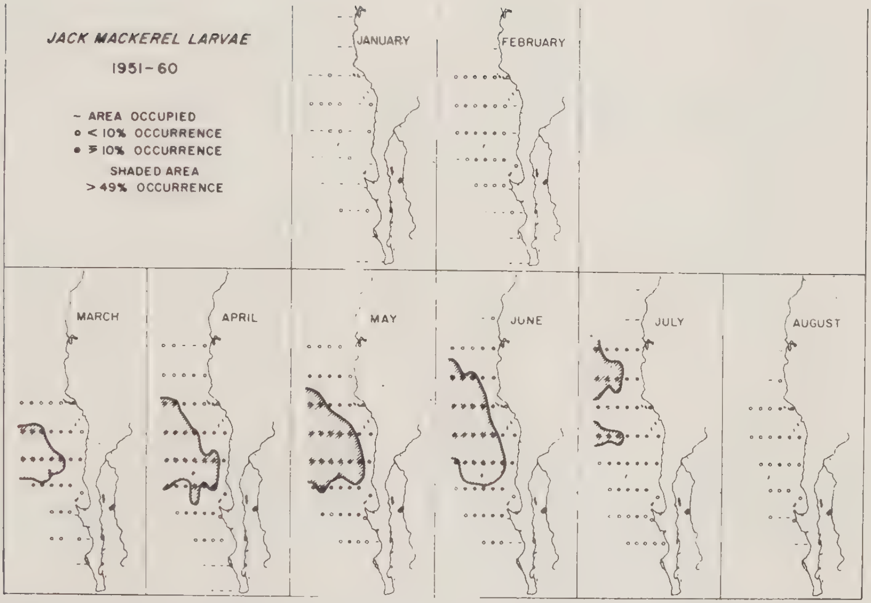

Figure 3.20. Average spawning position for the jack mackerel, Trachurus symmetricus, over a decade. (After Kramer and Smith, 1970)

the distance traveled is reduced 30%. It is recommended that a pilot-study survey with square grid be occupied and the alternative results from increasing rectangularity be analyzed for the optimum grid pattern.

3.3.2. Vertical Distribution

The determination of the extent of vertical distribution of a particular species is simplified by the observation that most pelagic spawning by fish occurs in the upper few hundred meters (Ahlstrom, 1959). Proper survey design is necessary to assure that the vertical distribution of spawning products and the subsequent movements of the eggs and larvae in the vertical plane will be delimited or described.

There are ecological and physiological aspects of vertical distribution. The ecological features, which involve the vertical coincidence of the fish larvae and their common food, competitors, and predators, are outside the scope of this manual. A physiological feature that is important in estimating spawning biomass is the temperature at which development is taking place. This information is necessary to calculate the residence time and abundance of the larvae. Thus, in ichthyoplankton surveys for spawning biomass estimates, the sample is taken from below the deepest larva (or at least through a consistent fraction of the larvae), and the larval abundance is reported as the number under a unit sea surface area (e.g., 10 square meters). This contrasts with ecological studies which report larva abundance as numbers per unit volume at given depths and which also require more precise temperature corrections for residence time.

A method for determining the proportions of larvae of a given species is illustrated in Table 3.16 and Figure 3.21 for anchovy and hake larvae collected in horizontally towed opening and closing Leavitt nets (Ahlstrom, 1959). Basically, the depth range is divided among the horizontal hauls by assuming that the mid-depth of each tow is representative for half the distance to the adjacent mid-depth above and below. At the surface, the upper tow represents depths all the way to the

Table 3.16. A method for estimating the depth distribution of anchovy and hake larvae.

REPRESENTED DEPTH (m)	DEPTH RANGE (m)	MID-DEPTH (m)	ANCHOVY				HAKE			
			N/1000m^3	N/10m^2	%	CUM. %	N/1000m^3	N/10m^2	%	CUM. %
0 -5	5	2	234	11.70	11.8	11.8	14	.70	0.7	0.7
5 -13.5	8.5	8	253	21.51	21.7	33.5	16	1.36	1.3	2.0
13.5-23.5	10	19	136	13.60	13.7	47.2	5	.50	.5	2.5
23.5-34.5	11	28	100	11.00	11.1	58.4	3	.33	.3	2.8
34.5-48.5	14	41	155	21.00	21.2	79.5	12	1.68	1.7	4.5
48.5-64	15.5	56	99	15.35	15.5	95.0	57	8.84	8.7	13.2
64 -80	16	72	19	3.04	3.1	98.1	346	55.36	54.4	67.6
80 -96.5	16.5	88	11	1.82	1.8	99.9	44	7.26	7.1	74.7
96.5-121.5	25	105	0.2	.05	.1	100.0	17	4.25	4.2	78.9
121.5-176.5	55	138	0	0	0		27	14.85	14.6	93.5
176.5-250	73.5	215	0				9	6.62	6.5	100.0
250 -320	70	285	0				0			
TOTAL TO 320 METERS				99.07				101.75		

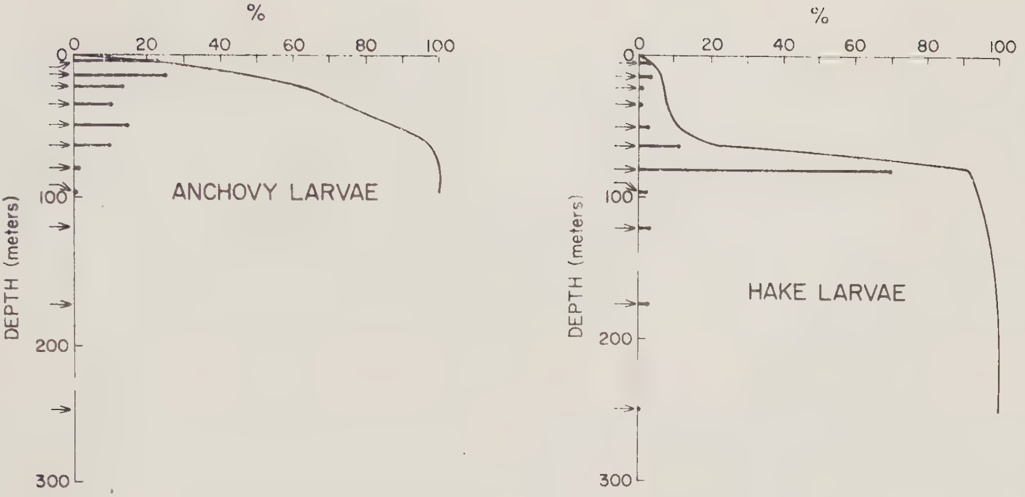

Figure 3.21. The depth distributions of anchovy larvae and hake larvae. The solid line is the cumulative percent curve and the individual bars at the indicated depths are the percent values of incidence. The arrows indicate the horizontal sampling levels. (From Ahlstrom, 1959)

surface . The lowest tow is assumed to represent as much depth below the mid-depth as above. The number of larvae per 1000m^3 at each depth is transformed to the number of larvae per 10m^2 sea surface area between the limits represented by the tow by the following equation:

$$C = C_V \left(\frac{SR}{V} \right)$$

Where C is the number per unit sea surface area; C_V is the number per unit of volume (234 anchovy larvae per 1000m^3); S is the unit sea surface ($10\ \text{m}^2$ in this example); R is the range of depth for the sample (5 m in this example); V is the unit volume ($1000\ \text{m}^3$ in this example). Thus anchovy between the surface and 5 m:

$$C = 234 \left(\frac{10 \times 5}{1000} \right) = 11.70$$

anchovy larvae per $10\ \text{m}^2$ from 0 - 5 meters depth. In this instance, the depth intervals are uneven. For some purposes, it is more convenient to use evenly spaced intervals. It now seems likely that stratification is more pronounced than earlier thought (Longhurst, 1967), which implies that much finer depth intervals than the above example will be necessary to increase the precision of depth distribution analysis. It is likely that the above type of analysis will suffice for determining the maximum depth of tow for species in the upper 300 meters.

3.3.3. Seasonal Distribution

Seasonal distribution of sampling will depend on the characteristics of the spawning season by species and the residence time of the spawning products in the sea. For example, sampling in polar areas can be expected to center around a brief spawning period with an extended residence time of planktonic stages. In tropical areas the sharp seasonal cycle may be absent and the residence time of the spawning products may be quite short. In temperate areas these characteristics are, of course, intermediate, with the added complexity that polar or tropical waters may actually be transported into the temperate areas to varying degrees. If a fishery on the target species exists in an area, gonad samples of the catch may be the best index of when ichthyoplankton surveys should be conducted. In the CalCOFI area, the four months January, April, July and October have been most routinely occupied with supplemental cruises made during the height (February, March, May and June) of

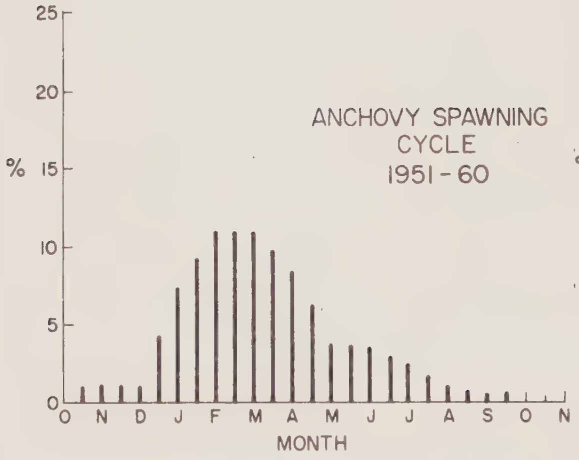

Figure 3.22. The spawning cycle of the northern anchovy, Engraulis mordax, in the California Current region.

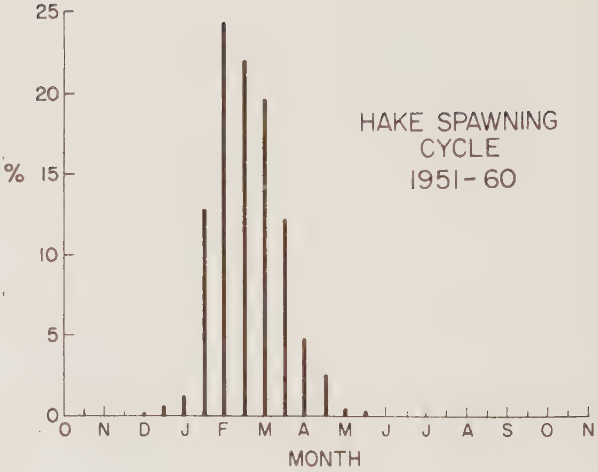

Figure 3.23. The spawning cycle of the hake, Merluccius productus, in the California Current region.

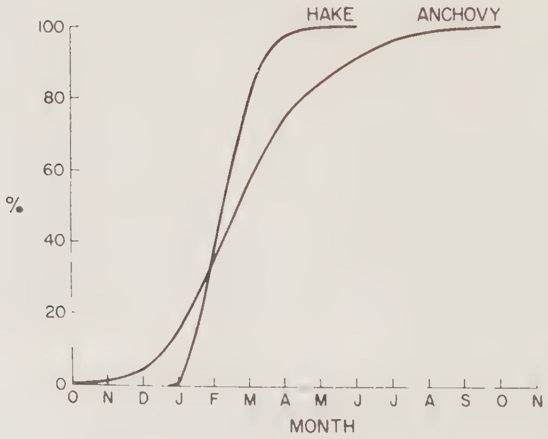

Figure 3.24. The cumulative percentage catch cycles of the larvae of hake and anchovy in the California Current region.

the spawning season of most species.

As in the case of geographic distribution, the purpose of monitoring is not to describe in detail the seasonal distribution of spawning but to get a representative sample of the spawning. For example, a monthly larval index for anchovy varies from a value of 5 to 112 with an average of 44. The larval index for four quarterly cruises is 48 for January, April, July and October, 42 for February, May, August and November, and 40 for March, June, September and December. The range of estimates is only 20% of the mean value for four cruises. For alternate monthly cruises, the larval index is 44 for the set of six cruises beginning in January and 43 for the six cruises beginning in February. The average anchovy spawning cycle is illustrated in Figure 3.22. Thus, four cruises conducted at three-month intervals would probably be adequate to sample anchovy, or similarly spawning species which have extended periods, for spawning biomass estimates. However, six cruises, two each quarter in the spawning season and one each quarter out of the normal spawning season, would assure a more precise estimate of spawning biomass.

The same monthly larval index for hake averages 28 and the three quarterly cruise possibilities are 20, 42, and 33. The two alternate month cruise series yield larval indices of 24 and 33. Thus, to adequately sample hake, or similarly spawaning species which have one or more brief spawning periods, requires more frequent and concentrated cruises. The hake spawning cycle off California is illustrated in Figure 3.23 and the cumulative percent frequency curve for anchovy and hake (beginning in October, the seasonal minimum for spawning) is shown in Figure 3.24.

For some species, the seasonal and geographic distributions of spawning interact and cause some sampling complexity. These cases are typified by the spawning that begins at one end of the range of the adult and spreads across the entire range by the end of the spawning season. The statistical difficulty in this case is that the survey cruise pattern may at times be conducted in the same direction that the spawning is spreading, thus apparently extending the spawning season by region. Conversely, the cruise may be conducted so that the stations are taken across the

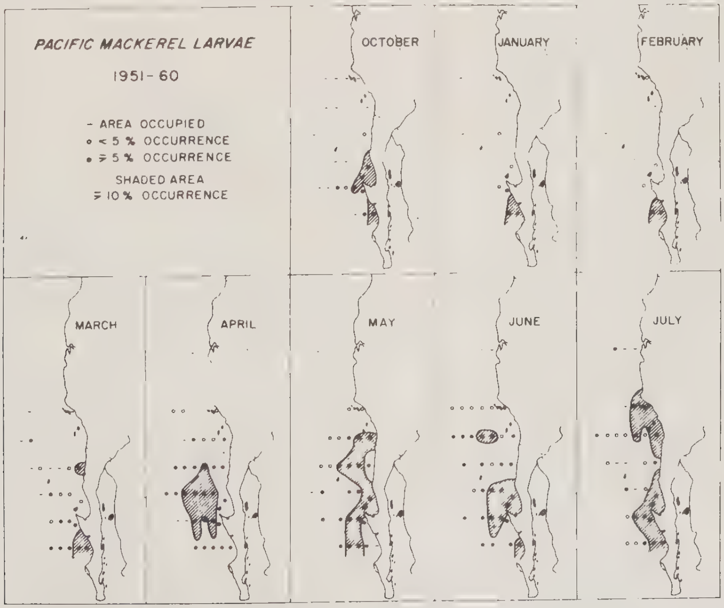

Figure 3.25. The spawning regions and seasons of Pacific mackerel, Scomber japonicus, in the most completely sampled months of the CalCOFI surveys. (From Kramer and Smith, 1970c).

area against the trend of spawning appearing to give a shortened season by region.

An example of incomplete seasonal coverage is shown in Figure 3.25. In this case, the Pacific mackerel (Scomber japonicus) is shown to be spawning in significant amounts in the region to the south of the survey area. It would be assumed that spawning was also occurring in the missing months of August, September, November and December. It is possible that the months of August or September could contain the peak spawning. Here, as in the jack mackerel example (Figure 3.20) the calculated spawning biomass is assumed to be minimal. These data have been collected incidental to ichthyoplankton surveys designed for the Pacific sardine and may be used to modify future surveys to enclose the Pacific mackerel spawning areas and times.

3.3.4. Oceanic Transport and Diffusion

Monitoring spawning biomass by ichthyoplankton surveys will normally include the sampling of several days' spawning products (Sections 3.4, 3.5). These data may be pooled to obtain an egg or larva regional census estimate (Section 2.4). It may also be important to estimate the transport of eggs or larvae into and out of the region. For example, regions that are transported from will exhibit an unnaturally high apparent mortality rate because older larvae have more chance of being transported away. This causes over-sampling in the "receiving" area. Figure 3.26 shows the characteristic lowering of the incidence of young larvae and elevation of the relative abundance of older larvae due to increased chances of being transported offshore.

The general problem of diffusion was treated by Hirano and Fujimoto (1968) and some preliminary calculations of the effect of diffusion on the statistical distribution of sardine egg samples have been made (Smith, 1973). Smith concluded that sardine eggs are spawned in a mosaic pattern of fish school dimensions, and the eggs at the perimeter subsequently disperse to a condition of randomness at the scale of the plankton sample. While an "average" condition leads to the dispersal of egg and larva patches with time, there is little information yet on the variability

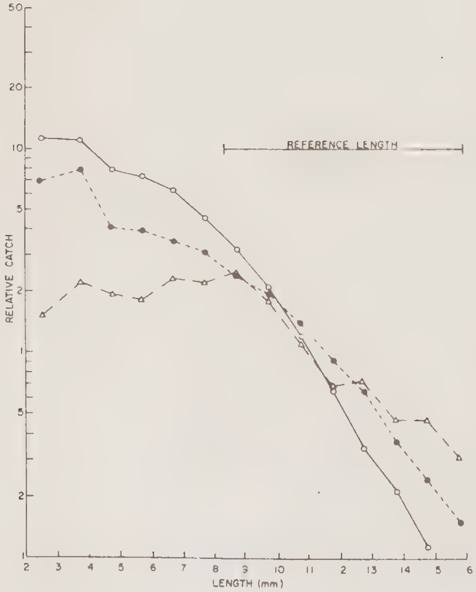

Figure 3.26. An example of a larva catch curve which has been influenced by transport of larvae away from the coast. (From Smith, 1972)

o——o catch curve of anchovy larvae near the coast

●---● catch curve of anchovy larvae 80 miles off the coast

Δ-.-Δ catch curve of anchovy larvae 160 miles off the coast of this rate. Slight variations in this rate could measurably alter the chances of getting or missing the occasional large samples which characterize the sampling of pelagic spawning products. Until this property is understood, it would be useful to measure an index of contagion. There are several, but perhaps one of the more useful ones is the "k" of the negative binomial series.

3.4. Sampling to Overcome Problems of Microdistribution

Some understanding of "microdistribution" is useful for interpreting the sample data from ichthyoplankton surveys. "Microdistribution" is defined for this manual as the distributional characteristics of organisms near the scale of their body size or range of movement in a short period. This is distinguished from "hydrographic distribution" which is the distribution associated with particular ocean features such as eddies, upwelling areas, or islands. Both are distinguished from "physiological distribution" which is the entire geographic and bathymetric area in which the organism can survive. These three levels of distribution might be equated with the terms "aggregation," environmental preference," and "tolerance."

Ichthyoplankton survey precision is determined by the scale and intensity of microdistribution of the fish eggs and larvae being sampled. These two factors are of primary importance in estimating the number of samples required for a unit precision of spawning biomass estimate.

Fish eggs and larvae, as Cassie (1968) noted, " . . . are among the more variable in their spatial distribution, probably because they are relatively short-lived members of the plankton, and are initially released in a high over-dispersed (patchy) pattern." In addition, there appears to be a great difference between the dispersal of the spawning products of a demersal fish, the plaice (J.W. Talbot, Lowestoft, U.K., personal communication) and a pelagic schooling fish, the sardine (Smith, P.E., 1973). It may be that the plaice, in a relatively fixed position, discharges its eggs into moving water, while the sardine drifts along with the water and spawns into a rather persistent patch.

Presumably patch sizes will range from the area of spawning of a single female, through the entire area of spawning activity associated with large scale hydrographic features. Thus, the spawning activity is the origin of the distribution pattern of eggs, but subsequent events may modify that pattern. The spawning products may be transported away from the spawning area (Hirano and Fujimoto, 1968), they may disperse from patch centers (Smith, P.E., 1973), and local or wide-scale water motions may concentrate them (Fig. 3.27) in convergences (Langmuir, 1938; Owen, 1966) or gyrals. Dispersal may also result in open spaces between eggs that are large enough for samplers to pass through even though they are inside a "patch". Spaces may also be created by localized sources of mortality such as starvation or predation.

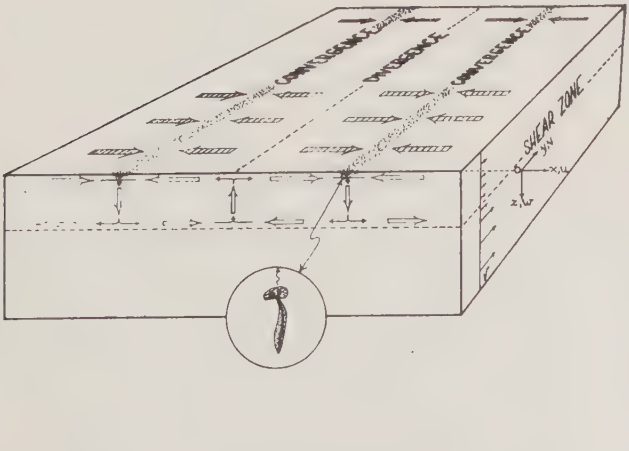

Figure 3.27. An example of a pattern-forming feature of the surface layer of the ocean which may interact with organism behavior to yield "strand lines" at convergences and areas of few organisms at divergences (Owen, 1966).

As yet there is no reliable way to measure the scale and intensity of pattern in the pelagic environment. Patch size can seldom be determined directly from the spawning products because they are not usually subject to direct observation or continuous measure-

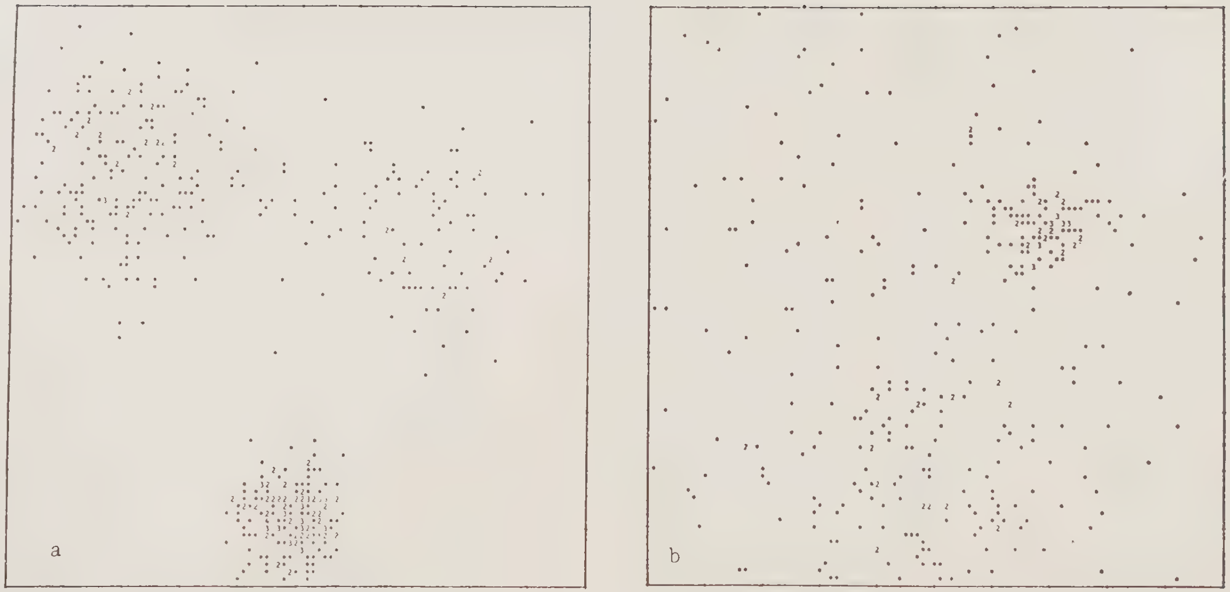

Figure 3.28. Computer simulated examples of centric aggregations. The mean concentration in (a) is 4.91 and the sample variance is 99.23. The mean concentration in (b) is 3.76 and the sample variance is 27.34. For comparison with the pattern in fish spawning, the "a" centric aggregation has an average negative binomial "k" of 0.256 and the "b" centric aggregation has a "k" of 0.600.

ment. Two indirect methods have provided a sense of scale of pattern. The first method, involving dispersal rate, was applied to sardine eggs by P.E. Smith (1973). The second method, involving sample size, has been borrowed from botanical techniques (Grieg-Smith, 1952; Pielou, 1969). Pattern has been described statistically by reference to the ratio of the variance to the mean (s^2/m) or some derivative of it such as the commonly used coefficient of variation (100 s/m). Lloyd's (1967) index of "mean crowding" also describes pattern and shows promise of distinguishing between various sources of mortality. Colebrook (1969) has shown that variance due to density gradients may be confused with patchiness.

Statistically, the best way, at present, to deal with the problems of microdistribution "is to increase the number of samples using the relationship S.E. = $S/\sqrt{n}$ where 'S.E.' is the standard error (standard error of the mean), and 'n' is the number of samples" (Cassie, 1968). An example is provided by the two computer simulated centric aggregations shown in Figure 3.28. These two distribution patterns differ in intensity but not in scale. For example, the above equation recommends that 411 samples be taken in order to get 10% accuracy in the mean concentration of the pattern in Figure 3.28 a. Only 193 samples need to be taken for the same precision in sampling the population in Fig. 3.28 b. The aggregation in Fig. 3.28 a has a mean density of 4.91, the sample variance is 99.23, and the average negative binomial "k" is 0.256. The aggregation in Fig. 3.28 b has a mean density of 3.76, the sample variance is 27.34 and "k" is 0.600.

3.5. Residence Time (Estimating Mortality)

One of the more difficult biases to measure in natural populations of eggs and larvae is "residence time" or period and extent of vulnerability to sampling. There are two simple techniques for measuring mortality which we will call the "cohort birth" method and the "constant birth" method. In the "cohort birth" method, the spawning products are released during a period of time which is short relative to the period of observation. The cohort (which refers to the group of eggs that is released at one time and whatever becomes of it) is then sampled in close successive time periods, and the mortality rate is estimated between each successive measurement. In the "constant birth" method, a single sample is analyzed for the abundance of a series of developmental stages of known age. It is beyond the scope of this manual to review all the necessary factors that effect these estimates such as drift of a cohort away from its point of origin (Smith, 1972), changes in the pattern and rate of dispersal (Smith, P.E. 1973), changes in the vulnerability of the larvae to sampling by day, night and size (Barkley, 1972; Lenarz, 1972, 1973; Murphy and Clutter, 1972) and the constancy of mortality rates among developmental stages (Fager, 1973). We will consider only the temperature-dependent hatching time (Ahlstrom, 1943; Lasker, 1964), the temperature-dependent larval growth rate (Lasker, 1964), and the food-dependent larval growth rate.

3.5.1. Temperature-Dependent Hatching Time

For annual estimates of spawning biomass, it may be necessary to make corrections for the temperature-specific hatching time because warm years speed the rate of development, reduce the residence times of the eggs, and cause an underestimate of the spawning population. Similarly, a colder-than-average year will cause the eggs to develop and hatch more slowly, thus increasing the length of time that eggs are vulnerable to sampling and causing an overestimate of the spawning biomass. The hatching time at various temperatures can be used to adjust the sample values to a central temperature and thereby correct the bias. The following table was developed from data provided by Lasker (1964) for Pacific sardine:

Temperature (j)	Hours to Hatch (t)	Resident Time Ratio (r)
13°	93.0	.65
14	78.5	.77
15	68.1	.88
16	60.2	1.00
17	53.7	1.12
18	48.4	1.24
19	42.2	1.39

Table 3.17. An example of the sample frequency distribution of Pacific sardine eggs and larvae.

CLASS BOUNDARY		EGGS			LARVAE (mm SL)						
LOWER	UPPER	A	B	C	3.00	4.75	5.75	6.75	7.75	8.75	9.75
1	4	7	14	5	13	5	12	23	21	32	23
4	16	14	14	16	36	20	32	51	52	19	12
16	64	20	27	31	50	46	68	45	18	8	2
64	256	36	33	17	29	49	30	7	1		
256	1024	22	25	26	23	34	3				
1024	4096	12	21	12	3	2					
4096	16384	6	5								
16384	65536	1									
	p	.645	.760	.591	.842	.852	.792	.689	.503	.322	.202
	n	118	139	107	154	156	145	126	92	59	37
	m	1044	734	385	153	189	54	22	13	8	6
	s	3465	1606	626	319	285	80	29	16	10	7
	k	.091	.209	.378	.230	.438	.457	.615	.648	.701	.715

In this instance, each sample value "x_{ij}" was multiplied by the residence time ratio "r_j" appropriate to each temperature "j" according to the following equation:

$$x_i = x_{ij}\ r_j$$

where x_{ij} = the number of eggs per 10 m^2 in the "i"th sample and its temperature "j", x_i is the $16^{o}C$ - specific equivalent number of eggs per 10 m^2, r_j is the ratio t_{16}/t_j, t_{16} is the duration of the egg stage, from spawning to hatching, at $16^{o}C$, and t_j is the duration of the egg stage at temperature "j" in the same time units as t_{16}.

3.5.2. Temperature Dependent Larval Growth Rate

Larval growth is dependent on temperature as well as food. In sardine, the food used in early growth comes from the yolk, as opposed to feeding success. Thus, a table showing the effect of temperature on growth from hatching to the formation of a functional jaw can be made based on work by Lasker (1964):

Temperature	Hours to Jaw Formation	Residence Time Ratio
(j)	(t)	(r)
13°	121.0	0.60
14	101.5	0.78
15	81.9	9.89
16	72.8	1.00
17	63.3	1.15
18	55.6	1.31
19	49.8	1.46

The equation for calculating the 16^{o}- equivalent abundance is the same as for hatching time (Section 3.5.1.). After formation of the jaw, the growth rate will likely

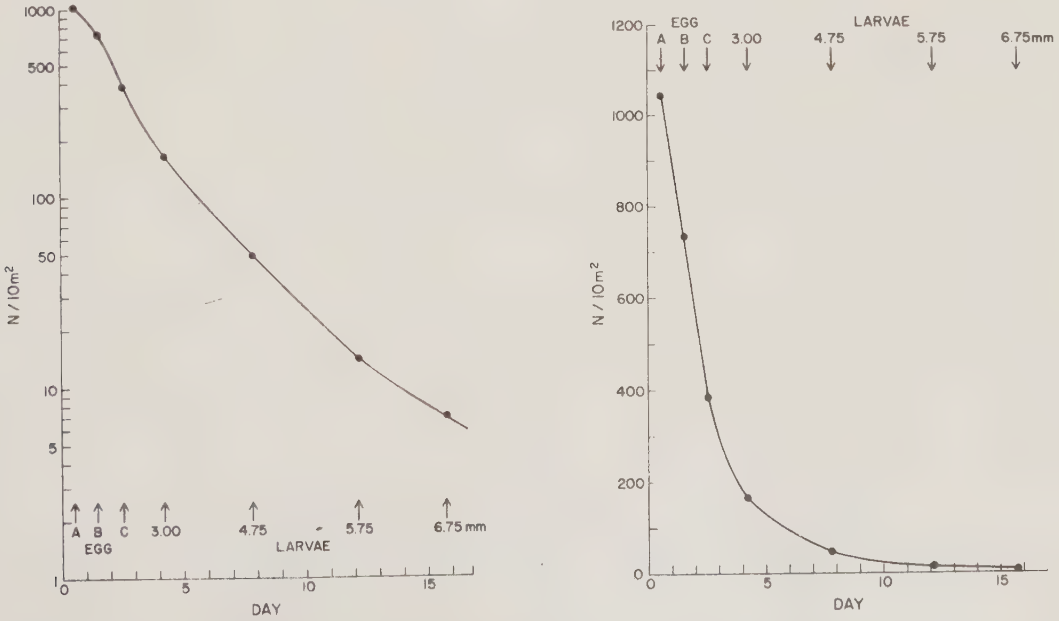

Figure 3.29. Apparent mortality rate of sardine eggs and larvae expressed on a logarithmic scale and an arithmetic scale (data from Ahlstrom, 1954).

be dependent on feeding success as well as temperature, which makes it more difficult to measure (Section 3.5.3.).

3.5.3. Food-Dependent Growth Rate

At present, there are no accurate methods for determining the food-dependent growth rate, nor for determining feeding-success in terms of abundance and composition of food particles in the field. "Cohort birth" methods of determining this value will be biased because of the probability that smaller members of the cohort, at the onset of feeding, will probably be more likely to starve than the larger larvae of the same cohort (Kramer and Zweifel, 1970). Also, the more active and larger larvae of a given cohort may attract more predation than the smaller more passive larvae.

3.5.4. Mortality Estimates

One attempt at deriving crude mortality rates was made by Ahlstrom (1954). These values illustrate one method of determining mortality rate:

	Eggs			Larvae			
	Early	Middle	Late	3.00	4.75	5.75	6.75mm
Individuals/$10m^2$	1044	734	385	395	234	56	22
Days at Stage	1	1	1	2.4	4.8	3.9	3.3
Individuals per day	1044	734	385	165	49	14	7
Age at mid-point	.5	1.5	2.5	4.2	7.8	12.15	15.75 days

Figure 3.29 illustrates this crude mortality rate on the logarithmic scale and the arithmetic scale. The data are derived from Table 3.17. At interpretation of an average line of this kind is that it represents "average" conditions relative to food and temperature. Future work on feeding and growth in the field may allow direct measurements of the food density and the interpretation of deviations from this crude mortality curve as explained by temperature and food density. Another bias was pointed out by Isaacs (1965). Since vulnerability to capture generally decreases rapidly in the feeding-larva stages, an explanation for increased catches of large larvae may be that those larvae which have starved become more vulnerable to capture. Further research is needed in the area of food-specific residence time, because growth may be arrested during starvation which leads to another unevaluated source of error.

3.6. Spawning Biomass Estimates

The fundamental relationship between the ichthyoplankton survey and the spawning biomass of a given fish stock is:

$$B = \frac{P}{C}$$

"B" is the spawning biomass of the fish stock, "C" is the census estimate of the egg production, and "P" is the capacity for production of eggs by a unit weight of fish stock. The production of eggs is determined by the fecundity of mature females expressed as eggs produced per unit time per unit weight and the proportion, by weight, of the mature stock made up of spawning females within each unit time. The appropriate census estimate of egg production is obtained by knowing the mean abundance of eggs in the spawning area, the mean residence time of the eggs in the water column, and the frequency of the egg census cruises.

The factors on which direct estimations of spawning biomass depend are not yet well enough known for most stocks to allow estimates of spawning biomass from ichthyoplankton surveys. The establishment of crude trial values for each parameter of fecundity and the subsequent refinement of these values to useful levels of accuracy and known levels of precision should be among the primary goals of ichthyoplankton research. Most of this manual is directed toward obtaining field estimates of egg production and analogous larva data from ichthyoplankton surveys. The procedures for determining population fecundity are not as well known and include the questions:

1) How many eggs are spawned by mature females per unit weight per unit time?

2) What proportion of the mature females are spawning at any given time?

3) How frequently does the average female spawn?

4) Over what period of time does each mature female in the population spawn once?

5) What is the seasonal distribution of spawning?

6) What is the geographic distribution of spawning by season?

7) To what degree does spawning rate or absolute fecundity depend on environmental conditions such as amount and availability of food?

8) What is the type and extent of variance for the above factors?

Until answers are found to the questions above, there are ways of obtaining preliminary estimates. The simplest (Smith, 1972) is to assume that the larval index is proportional to the spawning biomass alone. The equation of proportionality is then established using an independent estimate of spawning biomass, such as obtained by an analysis of the catch from each year class over the time it is in the fishery (Murphy, 1966). This simple equation is then used to extend the spawning biomass estimates into periods when the entire year class has not yet been captured.

Another method for estimating spawning biomass, is to determine the fecundity of mature females per unit weight and to arbitrarily assign a reasonable number of spawnings per year (Smith, 1972). This has been the primary approach of the ichthyoplankton surveys for the Pacific sardine. Analogous methods have been attempted for the northern anchovy. The important advantage of these preliminary attempts at the assessment of fish stock size is that they may be done with a minimum of information. The basic expense of these estimates is high for the primary species, but the addition of new species to the regional census is relatively inexpensive. If the general relationship between the larval index, or egg census and spawning biomass is sufficiently robust, the method will continue to provide a suitable check on catch analysis and lend supportive data for acoustic and aerial surveys.

3.7. Fecundity

The primary linkage between quantitative estimates of spawning intensity and coverage and estimates of the size of the spawning stock is fecundity (Saville, 1964). For new spawning surveys on relatively unfished stocks, it appears to be necessary to begin three phases of fecundity study. Before any fecundity studies have been done, the variations in spawning intensity are interpreted as changes of spawning biomass, fecundity and sampling error with the latter two assumed to be small relative to biomass changes. The first phase of the study of fecundity for the purpose of setting realistic limits to spawning biomass estimates is to determine the number of "advanced eggs" per gram of spawning female (MacGregor, 1968). The second phase is to determine the probability of a female attaining spawning condition by month or season. A third phase might be to understand the variations in fecundity from year-to-year, particularly in the number of batches spawned per year or alternatively the mean time between adjacent batches during the spawning season.

An example of the use of an egg or a larva census estimate with an independent estimate of the spawning biomass of a species was illustrated in Section 2. The time series of egg or larva census estimates may also be used alone to indicate time series trends in the relative spawning stock size. Estimates of absolute spawning stock biomass may be obtained if data exist on the egg production rate of females over a well-defined period (for example, a month or a year), the proportion of total spawning biomass which is male, the mortality rate of the eggs and larvae, and egg or larva census estimates which extend beyond the spawning region through the time of spawning.

Much of the fecundity information may be obtained from the catch through market sampling, from the incidental catch through sampling "trash fish" at sea, and similarly from exploratory surveys. The number of eggs per spawning per gram of female can usually be determined satisfactorily from a small sample (MacGregor, 1968). The biomass sex ratio can similarly be estimated from market or sea survey samples. MacGregor (1968) found the mean and standard error for 19 female anchovies was 574 ± 10% (95% fiducial limits) eggs per gram of spawning female. This would translate to 5.74×10^8 eggs per metric ton of female biomass per spawning. If the male biomass is 75% of the female biomass, the population fecundity rate should be the same number of eggs per 1.75 metric ton of adult, or 3.28×10^8 eggs per metric ton of adult per spawning. If the adults may be expected to spawn two to three times per year, the eggs ($X=2\frac{1}{2}$) would be 8.00×10^8 eggs per metric ton of adult per year.

Smith (1972) compared three hypothetical models of anchovy spawning to check the sensitivity of spawning biomass estimates to those uncertainties about the variability in spawning behavior in the context of the increase in spawning biomass of the northern anchovy. The first model postulated a stable relationship between the annual larval census and the spawning biomass. The second model postulated the single spawning of each female in the winter quarter and does not respond to subsequent variation in spawning in the remaining seasons. The third model postulated the single spawning of each female in a maximum quarter (winter or spring in this instance). There were no apparent differences in the estimation of spawning biomass but the annual figure was subject to the least variation and the "maximum" season was subject to the most variation. Thus, the annual figure was chosen as the most representative and stable.

In a similar evaluation of the Pacific saury (Smith, Ahlstrom and Casey, 1970), the bimonthly spawning maximum was chosen because of (1) clear shifts in the seasonality of spawning; (2) migration and spawning outside the survey area in some months; and (3) evidence from the transpacific stock of this species that the egg batches can be matured each two months. (Hatanaka, 1956)

The Pacific hake spawn only in the CalCOFI grid area in a sharp peak at the same time each year. Relative spawning biomass has been calculated by integration from December to April, cruises in January-February, and cruises in January, February and March. Relative to the natural fluctuation in the 1951-60 period, the errors of estimate from the less complete surveys appear to be satisfactory.

Advanced research on the fecundity-spawning season problem should be based on the spawning characteristics of the individual species or determined from ichthyoplankton surveys and inspection of adult gonads. The population and individual fecundity characteristics to be determined can be expected to vary by major fish group and by latitude. For example, more or less continual spawning might be expected in the tropics and highly seasonal spawning could be expected in boreal zones. If spawning is essentially continuous, the primary data to be considered is the egg production per gram of female per unit time. A single annual spawning survey would be sufficient for this spawning behavior. If each spawning female spawns a single batch of eggs in a well-defined season, then the biomass estimate is derived from a few surveys during the spawning season. The most complete surveys and data on individual fecundity and population spawning behavior are required when there is multiple spawning at varying times during the year and between years. The primary data required is the egg production per gram of female per batch of eggs and the minimum time between repetitive spawnings.

Fundamental research on spawning is required for the direct use of egg and larva surveys in the direct absolute estimate of spawning biomass of any given species. In many species, even indirect estimates of spawning biomass obtained from spawning surveys may be the best available for unfished or underutilized species.

3.8. Alternative Quantitative Ichthyoplankton Samplers

The "slow" Bongo net system is recognized here as the best type of sampler for use in quantitative ichthyoplankton surveys. However, other systems may be used and produce acceptable results, provided they are used in a rigorously specified routine. In many instances, results are comparable to those obtained by Bongos (Section 3.9.).

Some of these alternative systems have been in use for many years. Thus, it might be advisable to continue using an alternative sampling system, particularly if sampling performance has been well-documented over a long time period, until transfer to the standard equipment seems clearly advantageous. Also, there may be legitimate concern that the full-scale sampling system recommended here would be beyond the scope of the beginning ichthyoplankton program.

The major source of imprecision for each sampler will be the microdistribution pattern (Section 3.4.) of the eggs and larvae. Differences between samplers will primarily be related to volumetric sampling (Section 3.2.), i.e., volume and depth distribution of water filtered, the rates of avoidance in day and night tows, and the rates of escapement and extrusion through the meshes.

This section is not intended to describe these alternative samplers. (References are provided in the text.) Rather, the purpose is to review advantages and disadvantages of the major types of alternative sampling systems, relative to the Bongos, which may be used in quantitative ichthyoplankton surveys.

3.8.1. Oblique Tow Nets with Bridles

Many 1.0 m and 0.5 m nets have been designed and many are in use today. Descriptions of some of these are provided by Tranter and Smith (1968). One long-used example of this type of net is the CalCOFI net (Kramer et al, 1972) which consists of a cylindrical-conical net attached to a one-meter ring.

The chief advantage of this type of net is the simple and inexpensive bridle and ring used to launch and retrieve the net from the water. This process can even be done by hand, if necessary.

The main disadvantage, relative to the Bongo net, is the bridle preceding the net which causes directed water disturbances and results in increased avoidance. Problems associated with various types of materials used for the netting are discussed by Heron, 1968.

3.8.2. Vertical Tow Nets with Bridles

The first and most commonly used net which was designed to be towed vertically was the Hensen Egg net (Hensen, 1895; Simpson 1959, Santander and de Castillo, 1969).

Bridled 1.0m and 0.5m nets also fit into this category when hauled vertically. This type of sampling system is generally used in shallow depths.

The main advantage of vertical tow nets are: (1) simplicity in construction and (2) ease with which tow results may be converted to numbers of organisms per unit area of sea surface.

The chief disadvantage is the common practical limitation of equal sampling per unit depth. Other disadvantages include: (1) the sample is taken from water disturbed by the towing bridle all the way to the ship, thus avoidance may be great; (2) the rolling of the ship may alternately pull the net up rapidly and then let it fall, thus extruding organisms through the meshes on the ascent and expelling them from the mouth of the net on descent; (3) those nets having a small mouth restrict the size of the sample that can be taken.

3.8.3. High-Speed Nets

High-speed nets, designed to be towed faster than three knots, are still being developed and tested. Some standard forms have evolved (Fig. 3.30), e.g., the Gulf III (Gehringer, 1952, 1962) and modifications of it (Bridger, 1958; Nellen and Hempel, 1969; Zijlstra, 1970; Harding and Arnold, 1971). The newer high-speed nets appear to be satisfactory for estimating spawning biomass (Bjorke, Dragesund, and Ulltang, 1974; Gjosaeter and Saetre, 1974; Postuma and Zijlstra, 1974; Saville, Baxter, and McKay, 1974; Schnack, 1974).

One advantage of the high-speed type net is that it allows one to make headway to the next station during the tow, thereby saving ship time and money. Other

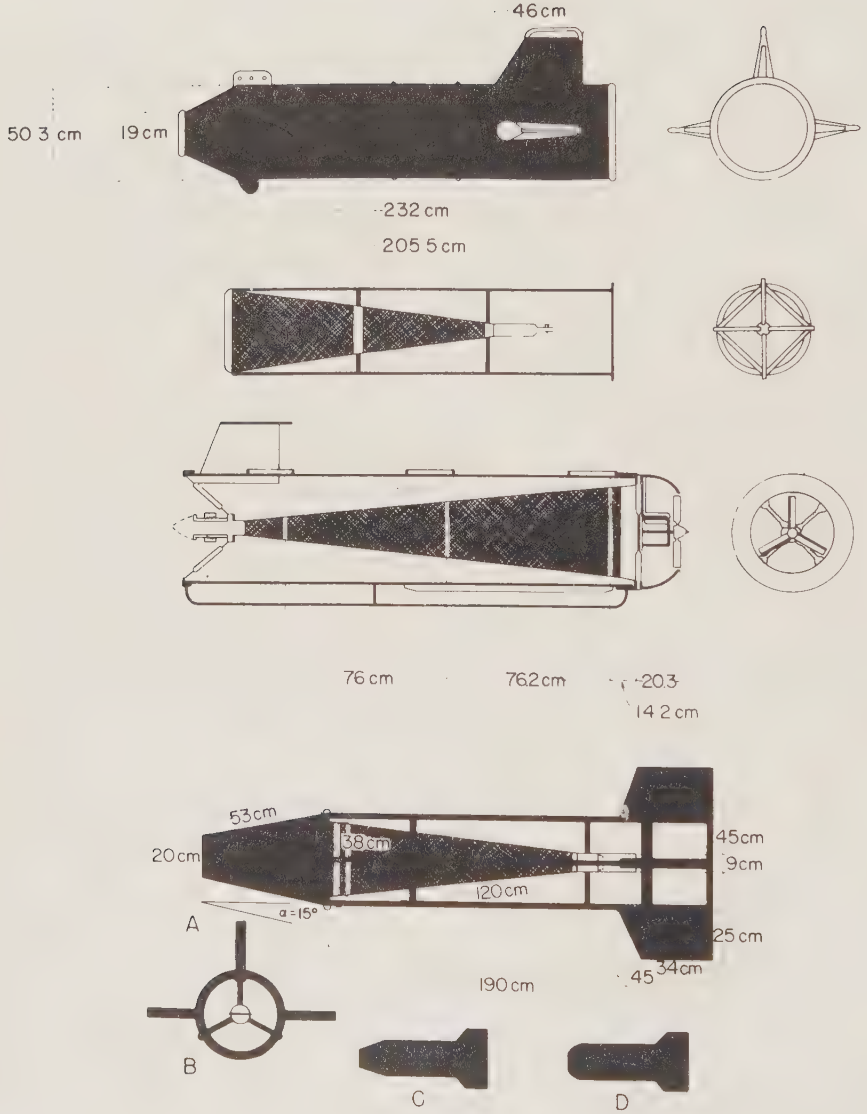
46cm
50 3 cm
19cm
232 cm
205 5 cm
76cm
76.2cm
20.3
14 2 cm
53cm
20cm
38cm
45cm
9cm
120cm
α = 15°
25 cm
A
45
34cm
190 cm
B
C
D

Figure 3.30. Scale drawings of three high-speed samplers used in the ICES (International Council for Exploration of the Sea) Larval Herring Survey Program in the North Sea. TOP) Dutch Gulf III (Gehringer, 1952; Bridger, 1958; Zijlstra, 1970) The net is of 0.4 mm nylon mesh and is suspended on the frame shown below the body of the sampler and the frame is inside the sampler body when under tow. MIDDLE) The Lowestoft High-Speed Plankton Sampler (Beverton and Tungate, 1967; Harding and Arnold, 1971) The net is of 0.3 mm nylon mesh. BOTTOM) German type high-speed net "Nackthai" (Nellen and Hempel, 1969) The net is of 0.3 mm nylon mesh. The net differs from the nets above by the absence of a casing surrounding the net. All three nets are fished at a towing speed of five knots and the double oblique tow to within five m of the bottom is accomplished by paying out and recovering the towing cable at ca. 20 meters per minute. The nets should have time depth recorders and flowmeters.

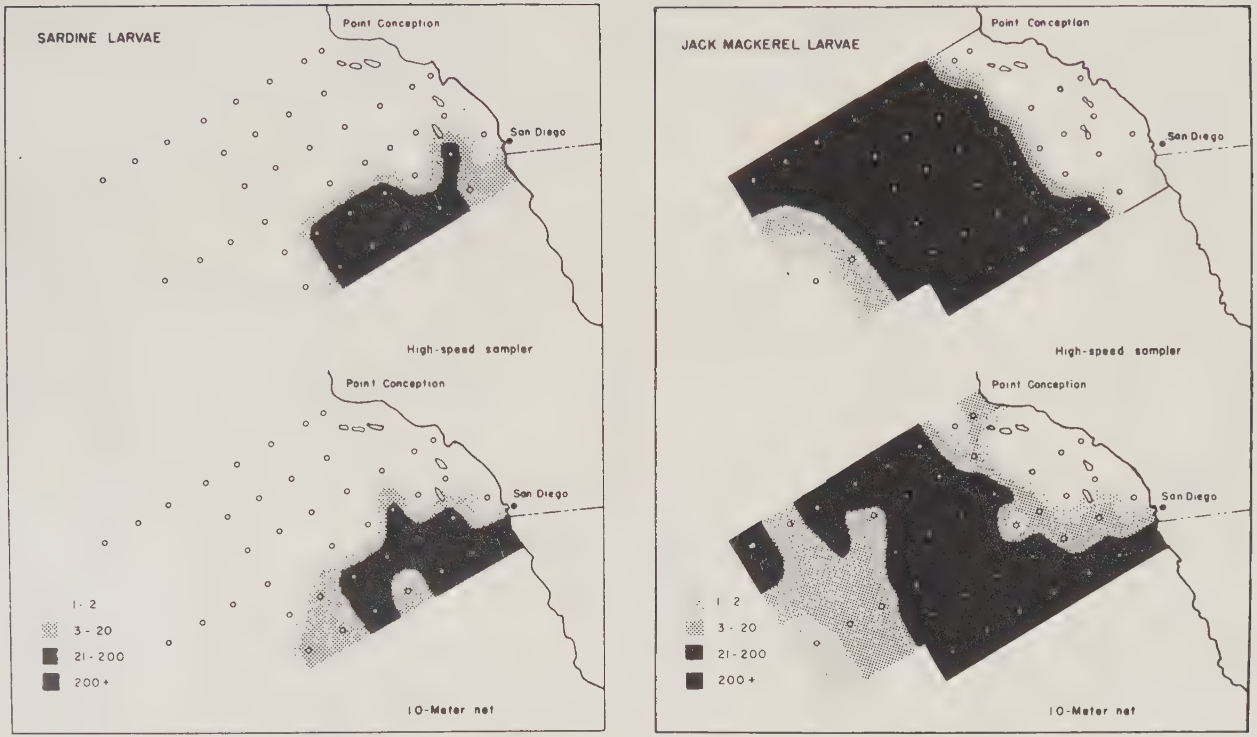
SARDINE LARVAE
Point Conception
San Diego
High-speed sampler
Point Conception
San Diego
1 - 2
3 - 20
21 - 200
200 +
10-Meter net
JACK MACKEREL LARVAE
Point Conception
San Diego
High-speed sampler
Point Conception
San Diego
1 2
3 - 20
21 - 200
200 +
10-Meter net

Figure 3.31. A direct comparison of results from two radically different ichthyoplankton samplers. Census estimates for sardine larvae were 477 x 10^9 for the CalCOFI one-meter net and 502 x 10^9 for the Isaacs high-speed sampler. Census estimates for jack mackerel larvae were 4.8 x 10^{12} for the CalCOFI one-meter net and 6.6 x 10^{12} for the Isaacs high-speed sampler. (Figure 9, page 198, and Figure 12, page 202 from Ahlstrom, Isaacs, Thrailkill and Kidd, 1958).

advantages include: (1) the speeds of tow are frequently high enough to allow sea current and wind conditions to be ignored and thus a rigorously controlled tow program is possible under severe sampling conditions; (2) larger specimens of the species are caught allowing mortality rates to be calculated for a larger portion of their planktonic life.

Disadvantages include: (1) filtration pressure is often high and variable which causes damage to and loss of smaller larvae; (2) the high speed requires a varying amount of cable for each increment of depth and this may make a straight tow path difficult, which could result in oversampling the surface waters; (3) the initial cost of the equipment and the more complicated methods of launch and recovery of the nets may be prohibitive for some ships and programs; (4) the small mouth sizes may not allow enough water to be filtered to pick up the larger rarer organisms which high-speed samplers are intended to catch.

3.9. Intercalibration of Quantitative Samplers

One may wish to intercalibrate samplers to allow comparison of (1) older data with that currently being collected, (2) cooperative surveys using different samplers, and (3) samplers which collect some overlapping size categories of ichthyoplankton. The standards of comparison should not differ from the statistical standards one applies to the survey results, therefore the estimation of the number of samples required can be derived from Table 3.6 (p. 52). The number of 'replicate' samples should be calculated from a trial series of samples with both samplers or may be estimated from the variance in the existing data from one of the samplers.

The intercalibration must account for all of the major sources of error: avoidance, escapement, extrusion, biased sampling of the water column, and different scales of sample size. Samplers should be compared under conditions which allow the comparison of the mean and variance per unit surface area and particularly the ability to detect the boundaries of the geographic distribution. For fish larvae, a comparison of the size composition of the catch is critical. It is unlikely that sample formats which change the scale of sampling radically will yield the same sample variance in comparisons and the services of a trained statistician should be sought for further tests of this phenomenon.

The complete results of a comparison of a high speed sampler with a 2.5 cm opening, towed in a horizontal series at 10, 20, 30, and 40 meters, and an oblique tow with a one-meter ring net towed from 70 meters to the surface is available in Ahlstrom, et al (1958). In this test, conducted over a 72,000 square nautical mile area in May of 1950, comparisons were made of total plankton volume, sardine eggs and larvae, anchovy larvae, jack-mackerel larvae, lanternfishes and other fish larvae. The horizontal distribution maps from this study are shown in Figure 3.31. From these comparisons one can see that the centers of abundance and distributional boundaries were well-represented by both nets. The high-speed net was ultimately rejected because it did not catch sufficient numbers of large larvae in its 40 m^3 sample relative to those caught by the larger slower net with a sample 10 times as large, and because the high-speed towing apparatus at that time was not capable of being fished to the depth required to sample under the distributions of larvae in this region. Nonetheless, the results from this comparison can be used to design adequate comparisons of standard sampler performance.

3.10. Design of Surveys to Minimize Costs

Table 3.18 lists the various cost elements of the CalCOFI surveys. Obviously, the increased efficiency of surveys must depend on reducing the major costs without substantially reducing the precision. Cursory inspection indicates that the greatest cost elements are shiptime, administration and technical personnel. Basic reductions in ship's costs can be made by: (1) reducing the number of cruises per year, (2) reducing the number of lines per cruise, and (3) reducing the number of stations per line. The recommended procedure is to conduct thorough cruise schedules in the exploratory and analytical phases of the egg and larva survey, then use the data from these phases to design the most effective and efficient monitoring cruises. It is possible that complete surveys need to be made only each two or three years with supplementary data being taken in the interim years.

Also, it may be convenient or necessary to merge sea operations of basic oceanography, exploratory fishing, acoustic surveys, pollution monitoring, or data buoy tending with the operations of egg and larva surveys. This can result in considerable savings in the sea-going phase of the egg and larva survey or alternately may provide extra samples with which to augment the standard survey. One must take precautions that the adventitious sampling program is an unbiased and representative set of samples. For example, one might need to adjust data from groups of samples taken only at night to compare with samples taken at all times of a 24-hour day. Samples taken over a small area may not be representative of a large area. Provided the sampling characteristics of the joint surveys are mutually satisfactory to the cooperators, massive savings are possible. For example, the CalCOFI surveys have profitted from this joint planning and conduct,and the potential now exists for the extensive environmental data to be used with the larval survey data to design experiments to test the relationships among stock size, larval survival, juvenile survival and recruitment.

Table 3.18. Estimated cost of a decade of ichthyoplankton surveys conducted over 300,000 square nautical miles of temperate, eastern boundary current off the west coast North America (CalCOFI 1972-base dollars).

CATEGORIES	PERSONNEL	DAYS/YEAR	$/DAY	YEARS	
DIRECT SURVEY COSTS					
Biological Aids	9	240	25	10	$ 540,000
Biological Technicians	34	240	50	10	4,080,000
Fishery Biologist	1	240	100	10	240,000
50 m Research Vessel	2	200	2500	10	10,000,000
SURVEY INTERPRETATION					
Fecundity Estimate					
Biological Technician	1	240	50	2	24,000
Fishery Biologist	1	240	100	2	48,000
Temperature Specific Hatching and Development Times					
Biological Technician	1	240	50	3	36,000
Fishery Biologist	1	240	100	3	72,000
Data Processing and Statistical Analysis					
Fishery Biologist	1	240	100	4	96,000
Biological Technician	1	240	50	4	48,000
Computer Time		240	2	4	1,920
Decade Total					15,185,920
Administrative Overhead (50%)					7,592,960
TOTAL					22,778,880

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7750

Surface Currents as Determined by Drift Card Releases Over the Continental Shelf Off Central and Southern California

JAMES L. SQUIRE, Jr.[1]

ABSTRACT

During March 1964 through February 1966, 8,320 plastic drift cards were released at selected points from an aircraft to measure surface current drift over two areas: from the coast to about 48 n.mi. off central California between Point Arena and Point Sur; and from the coast to about 90 n.mi. off southern California between Point Arguello and Punta Salsipuedes, Baja California, Mexico. The recovery rate was 3.5% in the central area and 5.7% in the southern area. An average 79.4% of the recoveries were found within 2 wk following the date of release. Results lend support to studies concluded by earlier investigators. The distribution of the directions from which drift cards were returned increased the evidence for the presence of an eddy off the coast between San Francisco and Monterey Bay during May through July, and of the large gyre and associated southern California countercurrent south of Point Conception during April through August and to a lesser extent in October and December.

INTRODUCTION

Dispersal and survival of the planktonic eggs and larvae of marine fishes in the ocean euphotic zone is affected by surface currents. The purpose of this study was to develop additional information on the drift patterns to which surface planktonic forms are subjected over the continental shelf of the west coast of the United States. The general direction of surface drift was determined and is compared with wind velocity during the survey period to expose any general relationship between wind direction and inshore surface currents. Johnson and Squire (1970) published the results found along the northwestern coast of the United States. This paper covers the central area from Point Arena to Point Sur, Calif., and the southern area from Point Arguello, Calif., to Punta Salsipuedes, Baja California, Mexico.

Field work for the study was carried out concurrently with an airborne infrared sea surface temperature survey of the continental shelf conducted with the cooperation of the U.S. Coast Guard (Squire 1971).

Increased interest in coastal surface currents as they may pertain to the drift of surface pollutants, such as petroleum, has prompted the documentation of this drift study.

METHODS

Talbot (1964) showed that specially prepared drift bottles could be successfully dropped from an aircraft; however, drift cards were chosen for this study due to the ease of handling and the limited space available in the aircraft. The individual drift cards are identical to those described by Johnson and Squire (1970) and were a 4 × 5¼-in, numbered, postage paid, self-addressed, fluorescent red postcard. A plain fluorescent red card was used as backing, and both were sealed in a clear plastic envelope with a steel washer as ballast. This study was conducted from March 1964 through February 1966, during which period 16 drift card releases were made off southern California and central California. From March 1964 through February 1965, airborne releases of drift cards were made once each 3 mo. Beginning in March 1965 and continuing until the end of the study, the frequency of drift card releases increased to one per month. Ten cards were released at each drop station.

The U.S. Coast Guard aircraft were flown at an average altitude of 500 ft over a prescribed pattern covering the central area to about 48 n.mi. offshore and the southern area to about 90 n.mi. offshore. Twenty-five release stations were located on the flight transects over the central area, and 27 release stations over the southern area. Dead-reckoning techniques, aided by the aircraft's tacan, loran, and radar navigation equipment were used to locate release points.

For visual comparison of wind direction, average wind speed, and the direction of surface drift, a wind rose symbol developed by Tabata (1961) was used on each drift chart (Figs. 1, 2). The symbols give the percent frequencies for the prevailing winds and calms (wind velocity 1 kn) based on eight points of the compass and the average wind speed in knots for a 2-wk period—1 wk before release and 1 wk after (drift cards were released on the last day of the first week of the 2-wk period). Wind data were obtained for geographical locations as near the

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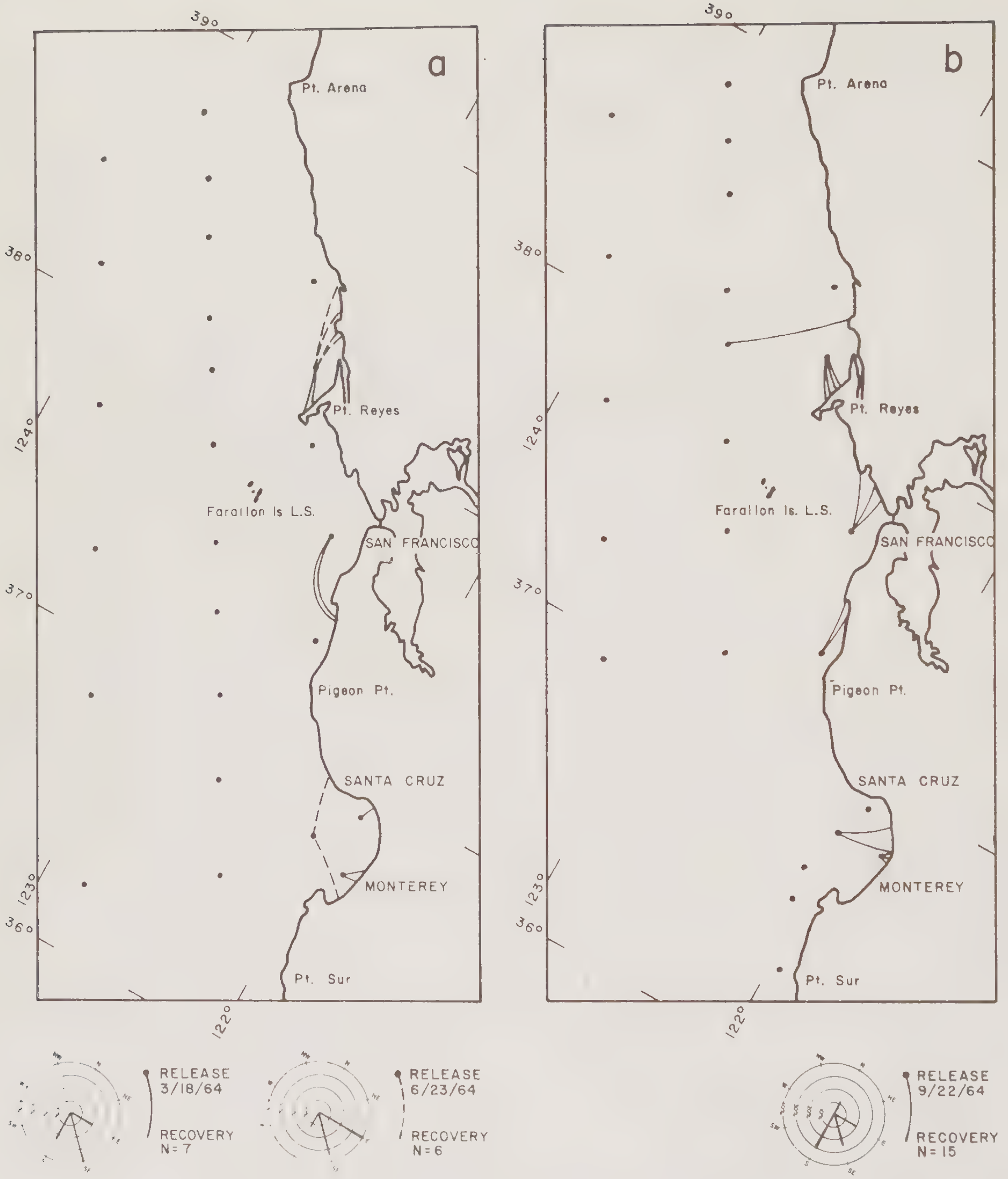
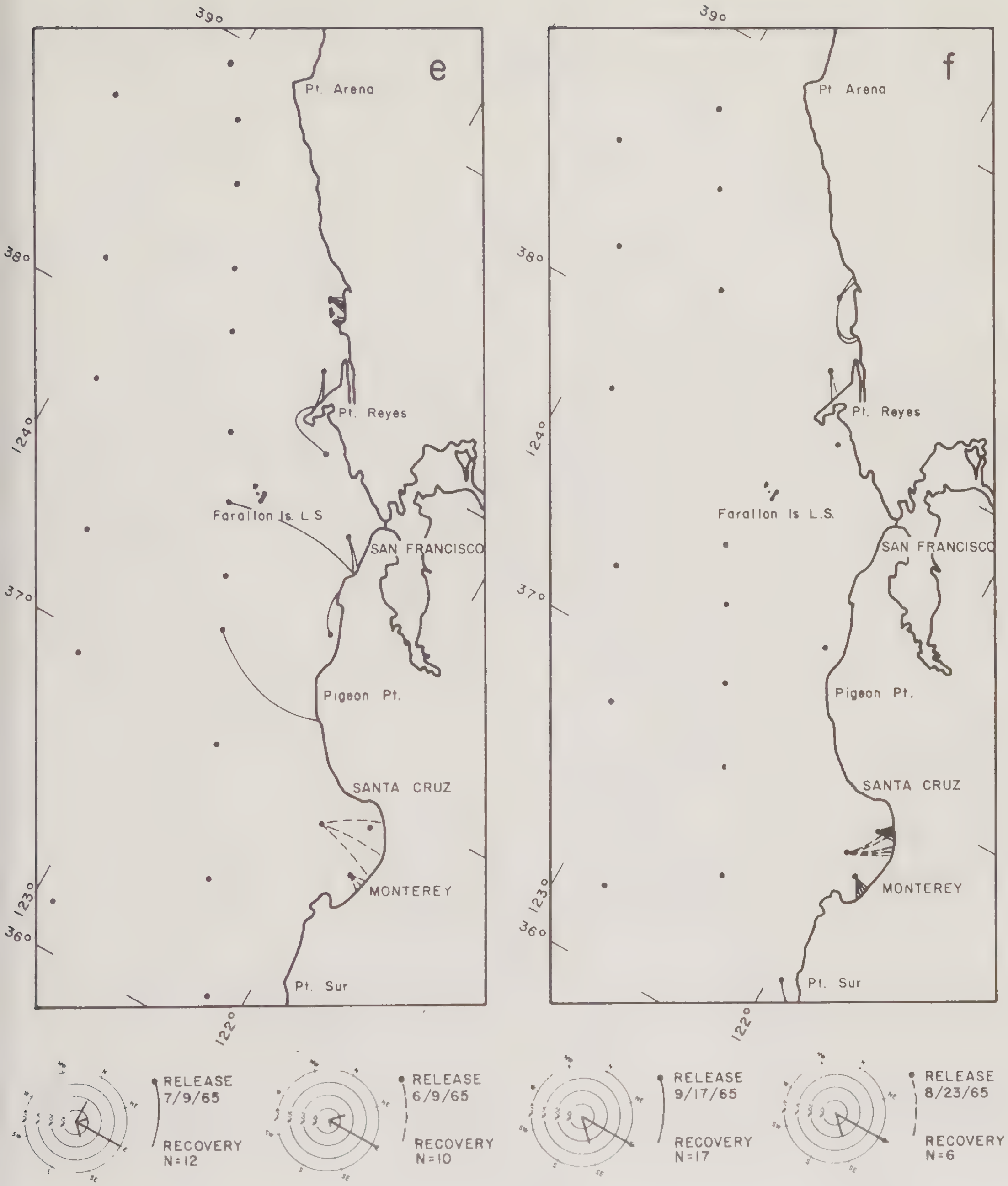

39°
a
Pt. Arena
38°
124°
Pt. Reyes
Farallon Is L.S.
SAN FRANCISCO
37°
Pigeon Pt.
SANTA CRUZ
MONTEREY
123°
36°
Pt. Sur
122°
RELEASE
3/18/64
RECOVERY
N=7
RELEASE
6/23/64
RECOVERY
N=6
39°
b
Pt. Arena
38°
124°
Pt. Reyes
Faralion Is. L.S.
SAN FRANCISCO
37°
Pigeon Pt.
SANTA CRUZ
MONTEREY
123°
36°
Pt. Sur
122°
RELEASE
9/22/64
RECOVERY
N=15

Figure 1.—Drift card release and recovery points off the central area of California: a) March and June 1964; b) September 1964; c) December 1964 and March 1965; d) April and May 1965; e) June and July 1965; f) August and September 1965; g) October and November 1965; h) December 1965 and February 1966.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Farallon Is L.S.
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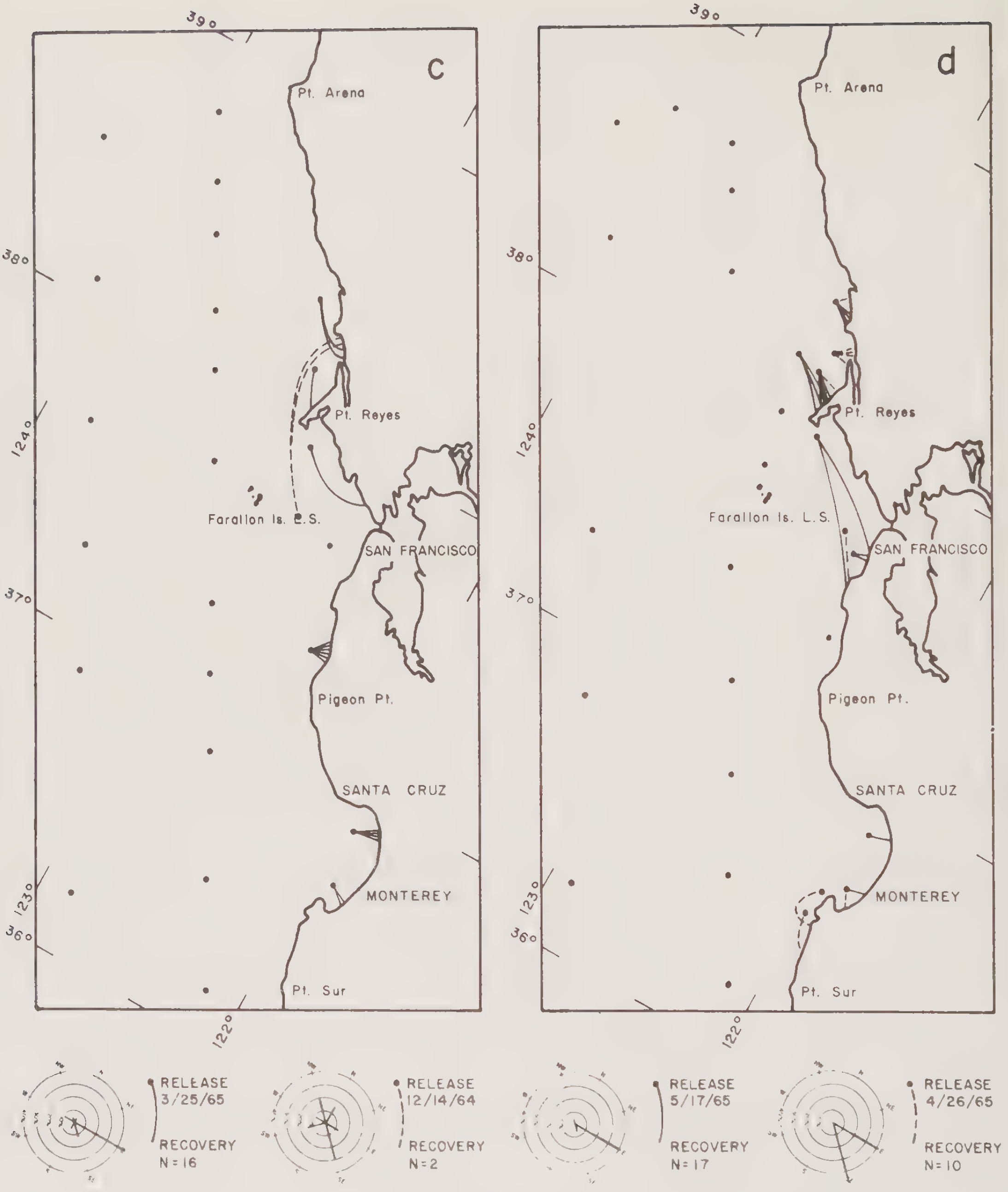
RECOVERY
N=6

Figure 1.—Continued.


c
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Pt. Arena
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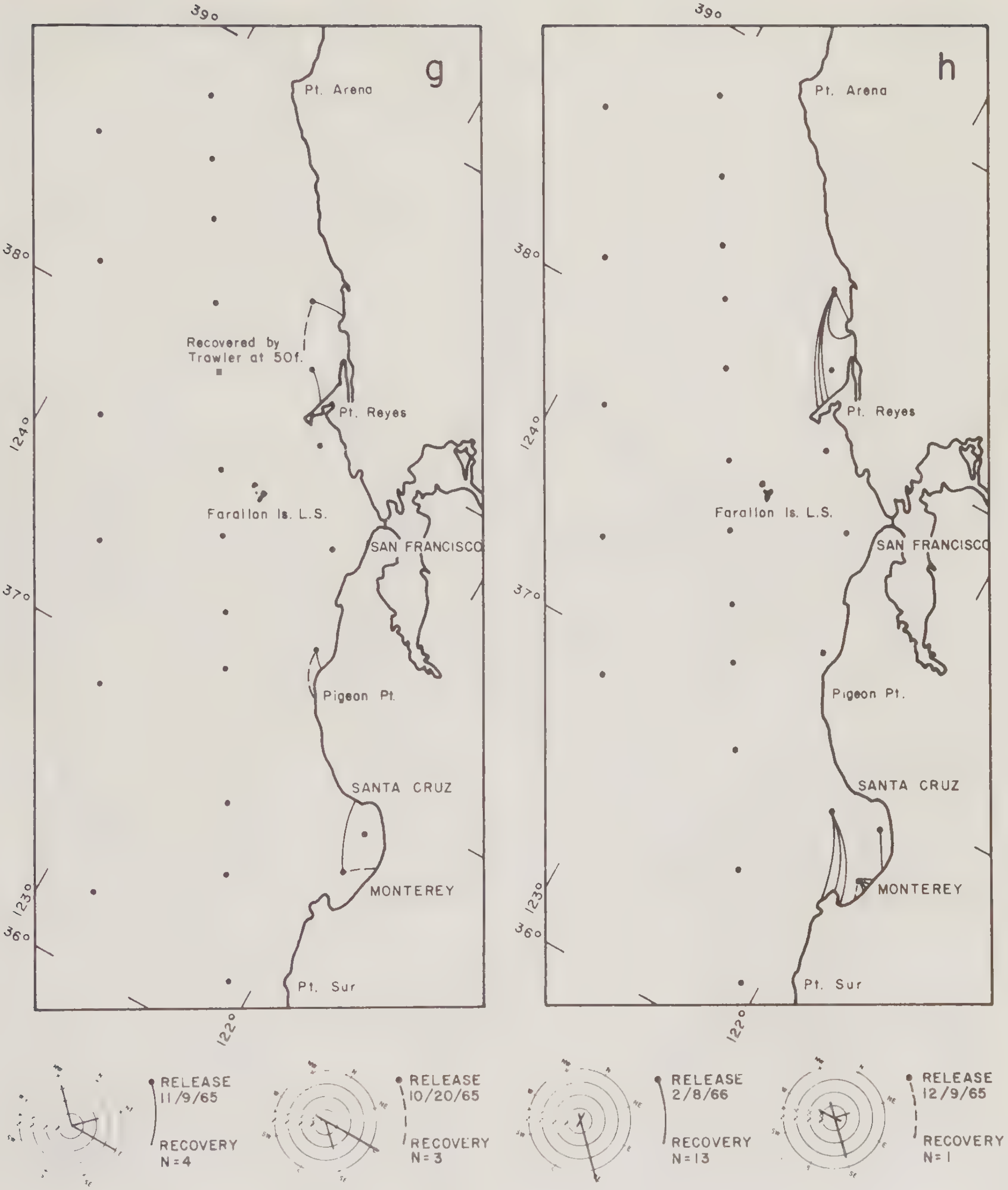
Farallon Is. L.S.
SAN FRANCISCO
Pigeon Pt.
SANTA CRUZ
MONTEREY
Pt. Sur
RELEASE 3/25/65
RECOVERY N=16
RELEASE 12/14/64
RECOVERY N=2
RELEASE 5/17/65
RECOVERY N=17
RELEASE 4/26/65
RECOVERY N=10

Figure 1.—Continued.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Recovered by Trawler at 50f.
Pt. Reyes
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Farallon Is. L.S.
SAN FRANCISCO
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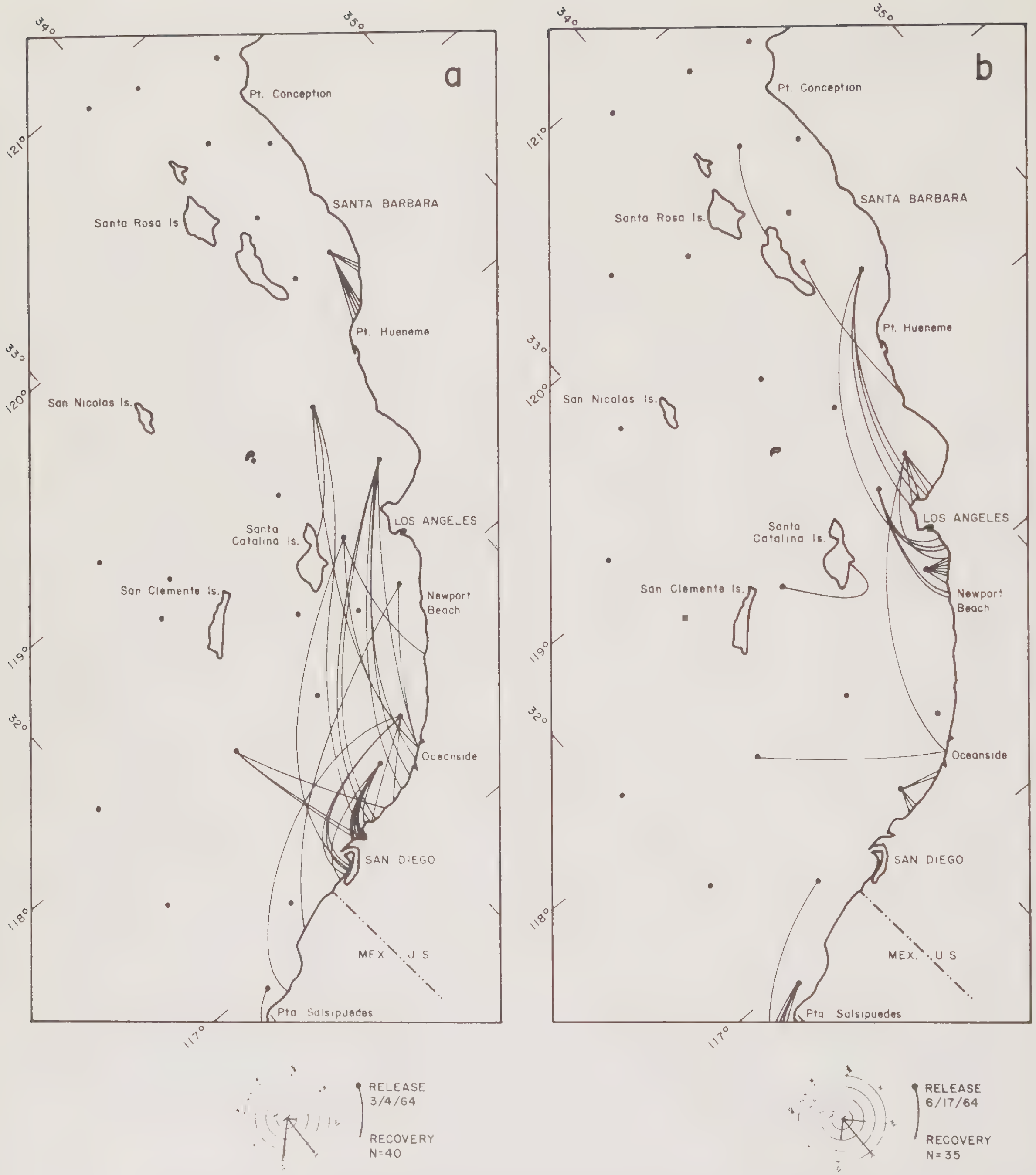
Pigeon Pt.
SANTA CRUZ
MONTEREY
123°
36°
Pt. Sur
122°
RELEASE 11/9/65
RECOVERY N=4
RELEASE 10/20/65
RECOVERY N=3
39°
h
Pt. Arena
38°
Pt. Reyes
124°
Farallon Is. L.S.
SAN FRANCISCO
37°
Pigeon Pt.
SANTA CRUZ
MONTEREY
123°
36°
Pt. Sur
122°
RELEASE 2/8/66
RECOVERY N=13
RELEASE 12/9/65
RECOVERY N=1

Figure 1.—Continued.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SANTA BARBARA
Pt. Hueneme
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Newport Beach
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RELEASE 3/4/64
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San Nicolas Is.
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SAN DIEGO
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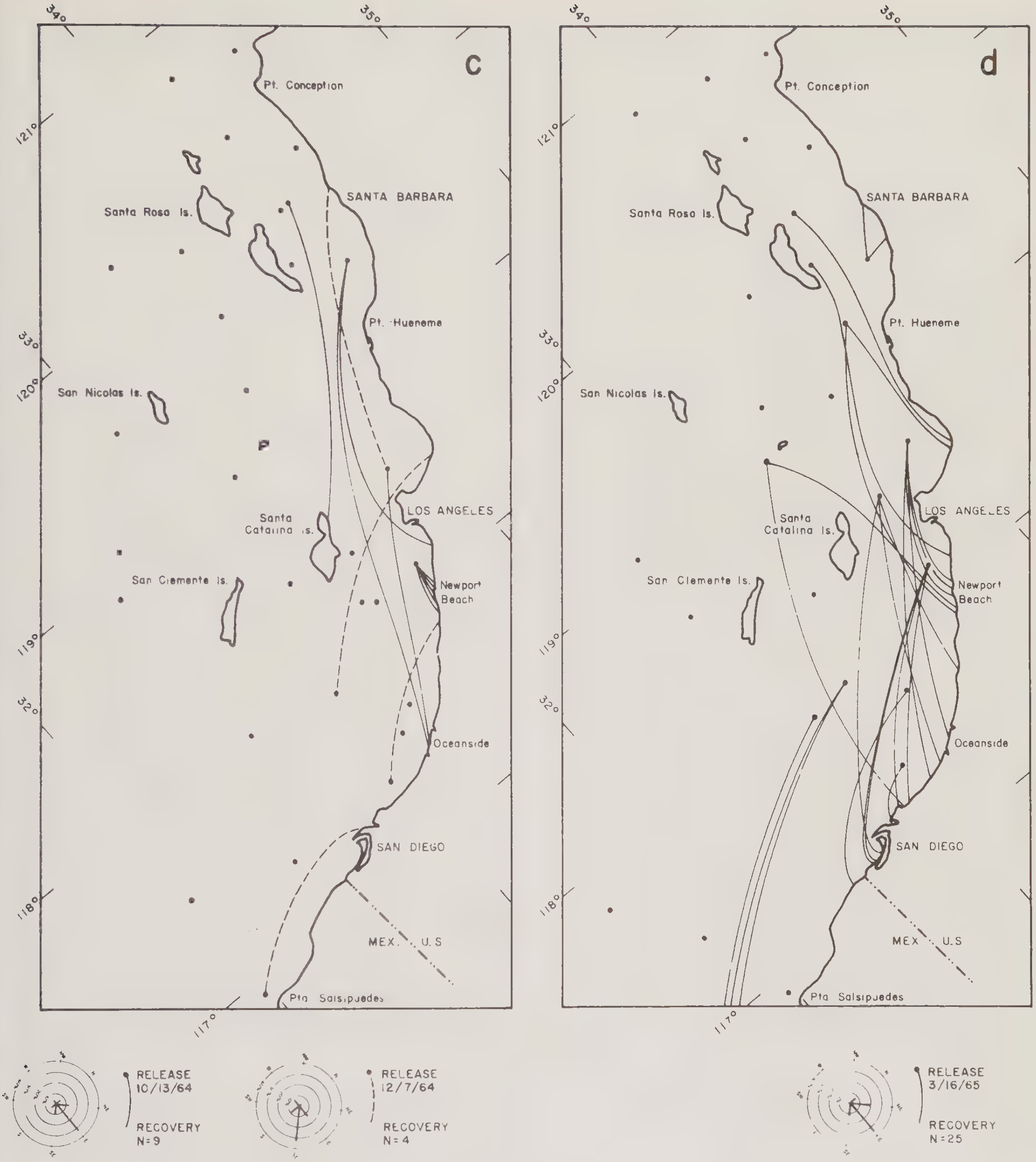
RELEASE 6/17/64
RECOVERY N=35

Figure 2.—Drift card release and recovery points off southern California: a) March 1964; b) June 1964; c) October and December 1964; d) March 1965; e) April 1965; f) May 1965; g) June 1965; i) August 1965; j) September and October 1965.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SAN DIEGO
MEX. U.S
Pta Salsipuedes
RELEASE 10/13/64
RECOVERY N=9
RELEASE 12/7/64
RECOVERY N=4
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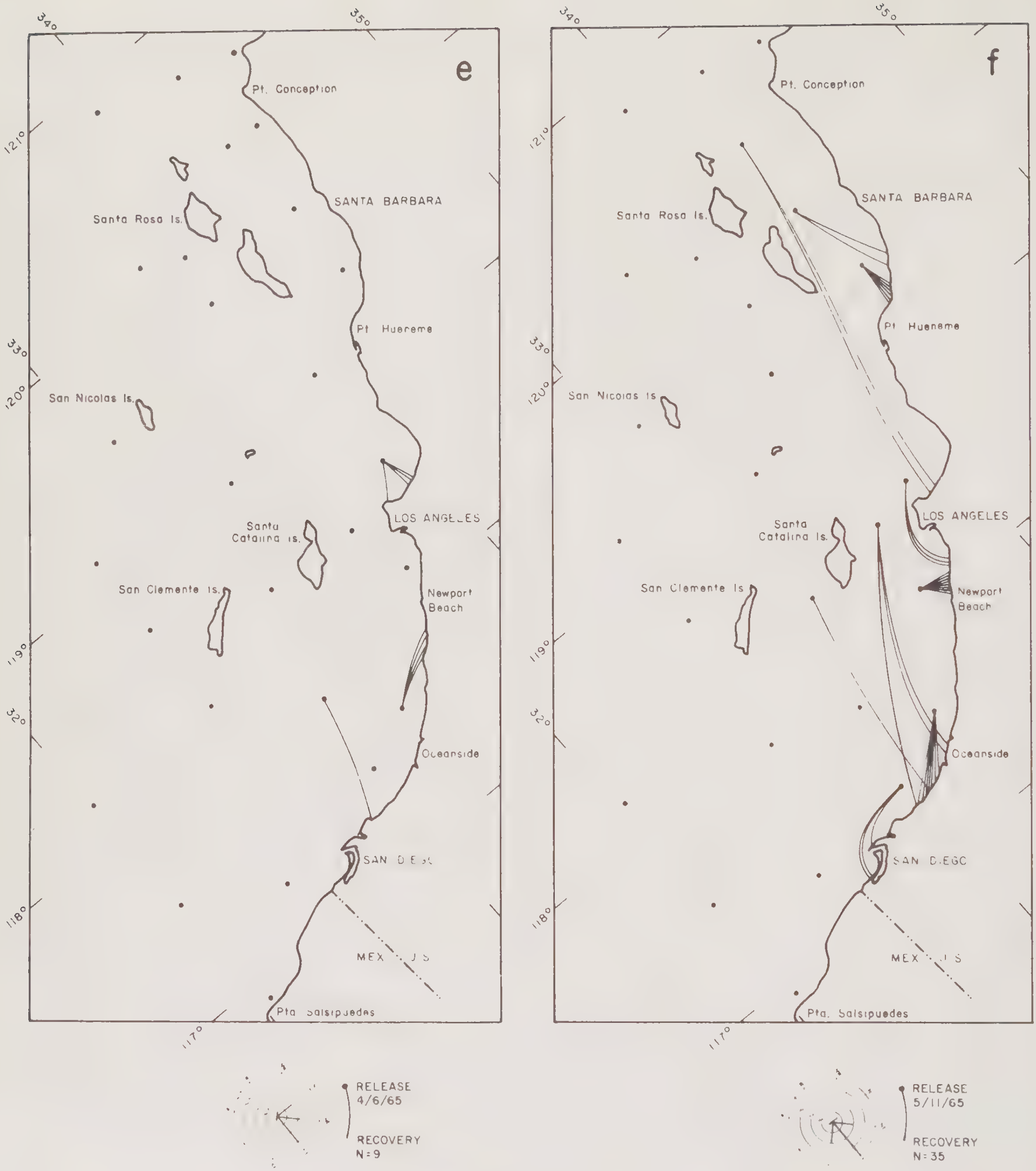
SANTA BARBARA
Santa Rosa Is.
Pt. Hueneme
San Nicolas Is.
Santa Catalina Is.
LOS ANGELES
San Clemente Is.
Newport Beach
Oceanside
SAN DIEGO
MEX. U.S
Pta Salsipuedes
RELEASE 3/16/65
RECOVERY N=25

Figure 2.--Continued.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Newport Beach
Oceanside
SAN DIEGO
MEX U.S.
Pta. Salsipuedes
RELEASE 4/6/65
RECOVERY N=9
f
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Pt. Conception
SANTA BARBARA
Santa Rosa Is.
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LOS ANGELES
Santa Catalina Is.
San Clemente Is.
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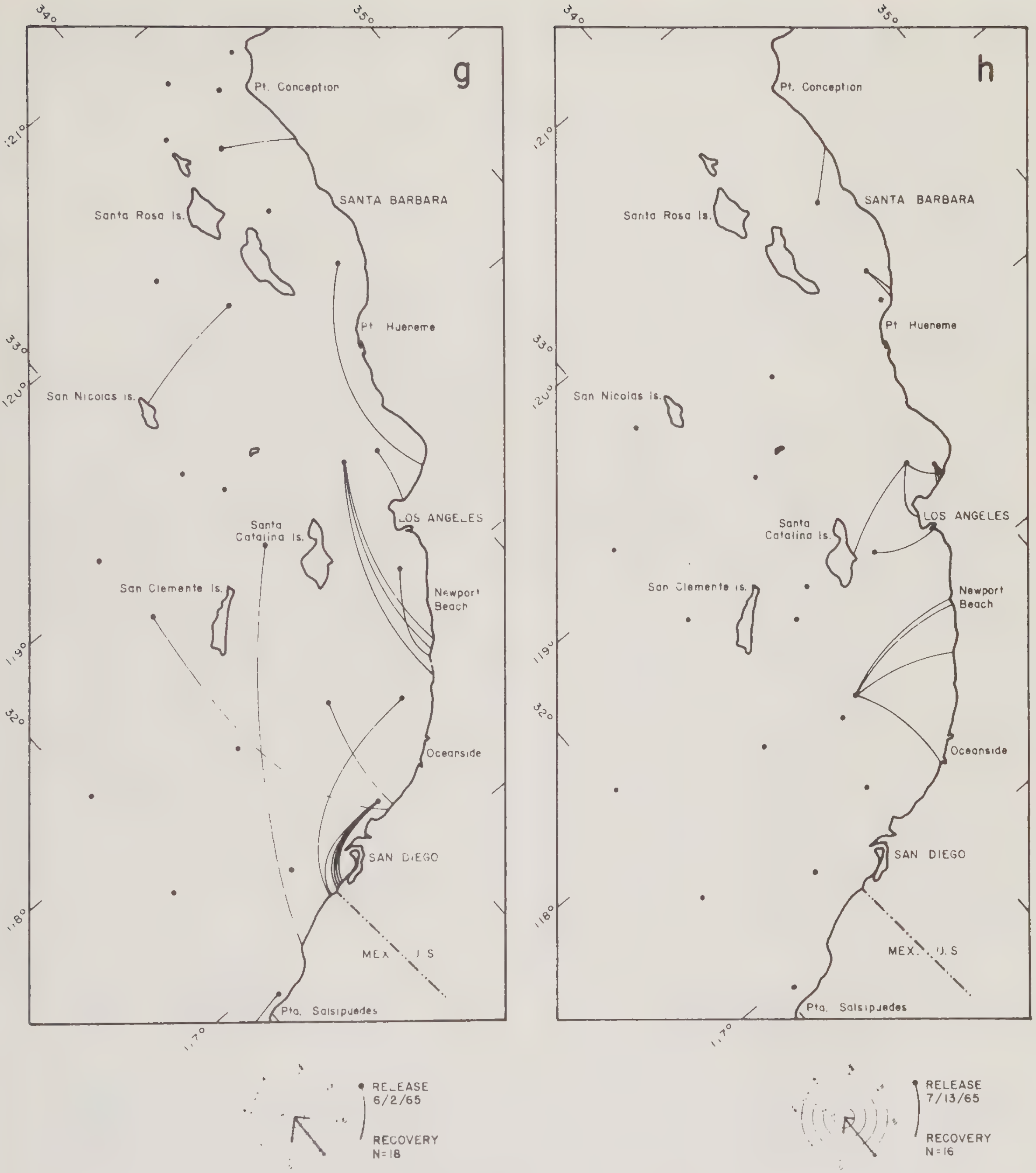
Pta. Salsipuedes
RELEASE 5/11/65
RECOVERY N=35

Figure 2.—Continued.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RELEASE
6/2/65
RECOVERY
N=18
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h
Pt. Conception
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Santa Rosa Is.
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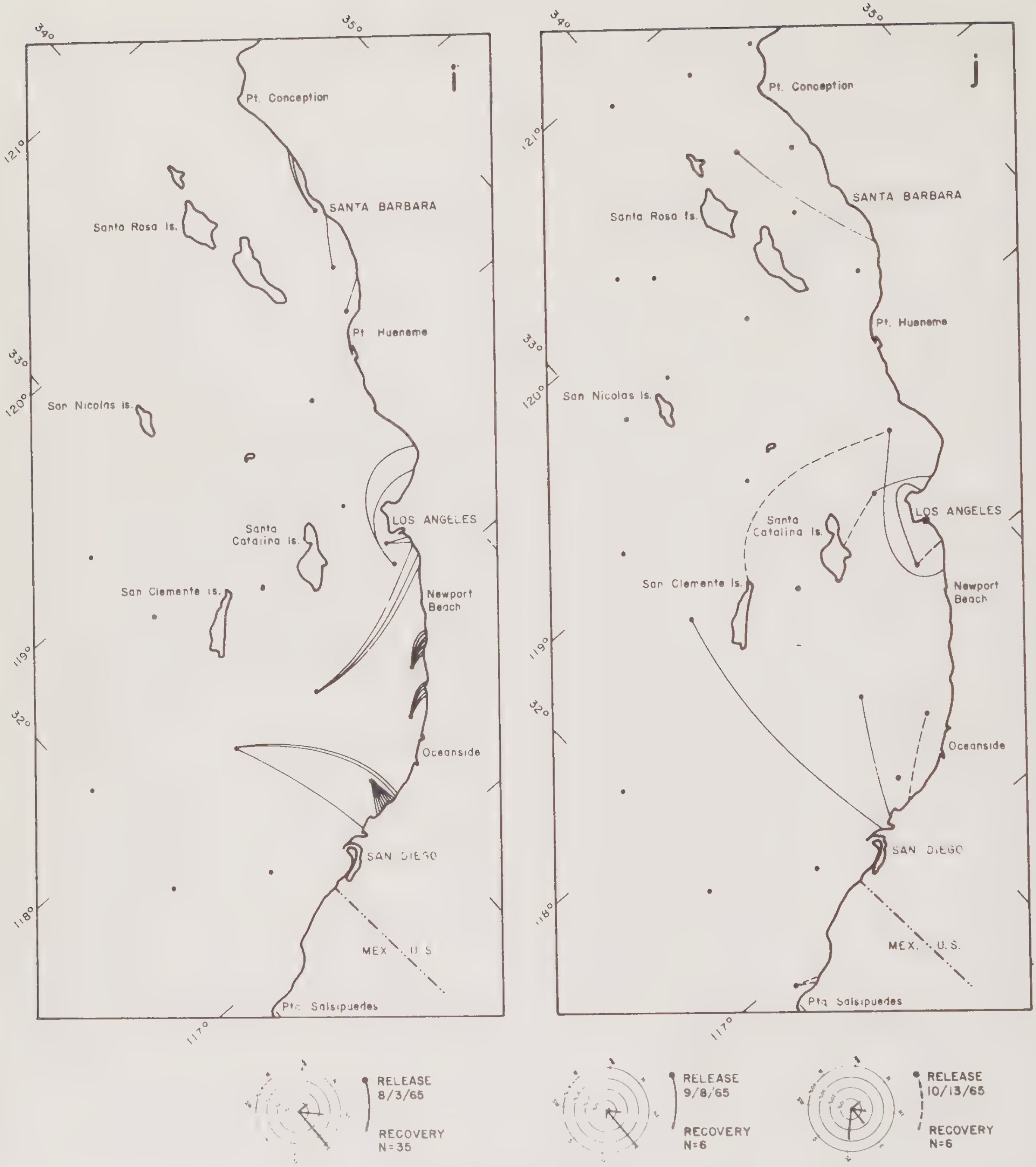
RELEASE
7/13/65
RECOVERY
N=16

Figure 2.—Continued.



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Newport Beach
Oceanside
SAN DIEGO
MEX.
U.S.
Pta. Salsipuedes
RELEASE 8/3/65
RECOVERY N=35
RELEASE 9/8/65
RECOVERY N=6
RELEASE 10/13/65
RECOVERY N=6

Figure 2.—Continued.

center of each survey area as possible. Data for the central area was obtained for the U.S. Coast Guard Farallon Island Light Station, 28 mi west of the entrance to San Francisco Bay, and in the southern area for the U.S. Navy San Clemente Island Naval Air Station. These data were made available by the National Weather Records Center, Asheville, N.C.

RESULTS

Of the 8,320 cards released over both study areas, 4.5% (377) were recovered. This recovery rate compares closely with those found by previous investigators using drift bottles and drift cards along the west coast of the United States (Tibby 1939; Schwartzlose 1964) and near Hawaii (Barkley et al. 1964). In the central area, 3.5% of the cards were returned, whereas 5.7% of the cards were recovered in the southern area. An average 59.8% of all cards recovered were found within 1 wk following the date of release, and 79.4% were found within 2 wk. The percentage of recoveries made during the first week after the drop in the central area was 72.1%, and in the southern area 52.7%. By the end of 2 wk, the percentage of recoveries in the central area was 86.8% and in the southern area 75.1%.

Charts (Fig. 1a to 1h central area, Fig. 2a to 2j southern area) giving the date and location of release and recovery and the average wind velocity were prepared for each quarterly and monthly drifter releases. The average wind speed was derived by averaging all values recorded during the 2-wk period. The rate of drift and trajectory of the card cannot be determined from the recoveries because of the lack of information between time of release and recovery. Original data to determine the time between release and recovery is not available. No recoveries were made and no charts were drawn for southern area releases in November and December 1965 and January and February 1966; nor for the central area during January 1966.

DISCUSSION AND CONCLUSIONS

The patterns of current flow associated with the California Current along the North American west coast have been examined by a number of scientists (e.g., Tibby 1939; Sverdrup et al. 1942; Reid et al. 1958; Burt and Wyatt 1964; Schwartzlose 1964; Tully 1964). We would expect the surface drift in the nearshore areas generally to be in agreement with the findings of these scientists.

Drift card recovery rates probably bear a relationship to the amount of shore activity by people. Many areas of the coast in the central area are rocky and not easily accessible. This, and the fact that the coastal population is small, would account for reduced returns when compared with southern California. The southern California coast is easily accessible, except for the island areas, and there is a high population level along most of the coast and from this a higher recovery rate would be expected.

Most of the recoveries in the central area were from drop stations relatively close to shore. Only three recoveries were from the line of drop stations located about 25 mi offshore, and none were recovered from the outer line of stations, about 50 mi offshore.

Southern California recoveries were mostly from stations near the coast, between the coast and Catalina, and the Santa Barbara Channel Islands; few recoveries were from the offshore drop stations.

Drift cards recovered along the coasts of central and southern California gave evidence of some surface drift toward the east and/or southeast through most of the year. Only in December 1966 did neither area have at least one return from either direction. Five of the 15 mo in the central area and 6 of the 12 mo in the southern area had a significantly greater proportion of the recoveries from the east and/or southeast than from all other directions combined.

Off the central area, little evidence of a strong Davidson Current can be observed along the open coast during the late fall, winter, or early spring months [Fig. 1a, 1c (March), 1g (November), 1h (December, February)]. Only in December 1964 (Fig. 1c) does evidence of the coastal countercurrent exist, with recoveries from off Bodega Bay from drift cards dropped near the San Francisco light vessel. Schwartzlose (1964) had indications from his work that an eddy flowed counterclockwise during the summer between San Francisco and the north edge of Monterey Bay. In July 1965 (Fig. 1e), off Halfmoon Bay and south of Point Reyes, some of the recoveries indicated a northward flowing coastal current during this period. During the remainder of the year, most of the recoveries showed drift to the east and/or southeast.

In the southern area between Point Conception and northern Baja California, an average 69% of the drift cards recovered had moved in an east and/or southeast direction. These observations reflect the combined influence of northwest winds and the relatively permanent southerly flowing current reported by Schwartzlose (1964) off the southern California and Baja California coasts.

Evidence for the gyre south off southern California was found during the late spring and summer (Fig. 2b, 2e, 2h, 2i). Some of the returns from coastal areas were recovered northeast to northwest of release points and these recoveries were most evident along the coast from San Diego northward and offshore to the San Clemente and Catalina Islands and the Los Angeles area. During these months Tibby (1939) reported that south flowing offshore currents return along shore as the north flowing Southern California Countercurrent. Forty percent of the returns from the August 1965 (Fig. 2i) releases drifted north or northwest nearly 90° from the prevailing winds flowing toward the east-northeast. Returns from the December 1964 (Fig. 2c) drift cards lend support to the conclusion by Reid et al. (1958), that the northerly flowing countercurrent associated with the large eddy off southern California is present in some measure through the late fall and winter.

ACKNOWLEDGMENTS

I thank Stuart N. Luttich, Gerald B. Talbot, and Sven I. Johnson for assistance in the study and to express appreciation to the U.S. Coast Guard Air Stations at San Francisco and San Diego, Calif., whose cooperation helped make this study possible.

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EFFECTS OF BENZENE (A TOXIC COMPONENT OF PETROLEUM) ON SPAWNING PACIFIC HERRING, *CLUPEA HARENGUS PALLASI*

JEANNETTE W. STRUHSAKER[1]

ABSTRACT

When female Pacific herring were exposed to low (parts per billion) levels of benzene for 48 h just prior to their spawning, a significant reduction occurred in survival of ovarian eggs and resultant embryos and larvae through yolk absorption. The reduction in survival of ovarian eggs was approximately 10-25%, for embryos from fertilization to hatching, 26%, and for embryos and larvae through yolk absorption, 43%. Exposure to benzene also induced premature spawning and resulted in aberrant swimming behavior and disequilibrium in adults of both sexes.

The maximum accumulation of ^{14}C-labeled benzene and/or metabolites in ovarian eggs (14 times initial concentration in water in 24-48 h; 1.4 μl/g from 0.1 μl/liter) was greater than in later egg and larval stages as measured in other experiments.

Conservatively estimating the total reduction in survival in these experiments to be approximately 50% through yolk absorption, I surmise that the effect of exposing spawning herring to only one toxic component of petroleum could have a significant effect on the population. The fish in these experiments were exposed to relatively high parts per billion levels, but they were exposed for a relatively short period (48 h); it is probable that in the estuary, if chronically exposed over a longer period of time to low parts per billion levels of aromatic components, the populations could be seriously affected.

When the spawning female herring is compared with other life history stages, we find that the spawning stage is clearly the most sensitive of those tested. If fishes prove generally to be most sensitive to petroleum components during their spawning seasons, fishery management decisions should take this factor into consideration in protecting the resources.

In studies of pollutant effects on marine organisms, emphasis should be placed on critical or sensitive life history stages. With this in view, research on petroleum effects on fish has been directed more recently toward egg, embryo, and larval stages (Kühnhold 1969, 1972; Evans and Rice 1974; Struhsaker et al. 1974). Results in many studies revealed that fish egg and larval stages were surprisingly resistant to crude oil and water-soluble and aromatic fractions of crude oil. Some of this resistance in fish is probably attributable to the presence of enzymes for metabolic detoxification of components with ensuing rapid depuration and physiological homeostasis (Lee et al. 1972; Neff 1975; Korn, Hirsch, and Struhsaker 1976, footnote 2).

I have observed, as expected, that the effects of exposure of monoaromatics such as benzene are more severe at all life history stages if fishes are otherwise stressed by environmental extremes or are in poor "condition" from inadequate nutrition. On this basis it is suggested that the female at time of spawning may be the most sensitive stage to toxic oil components. In herring, for example, the fish often feed poorly for some time prior to spawning and have low fat and energy reserves associated with the production of eggs (Blaxter and Holliday 1963). Anadromous fishes or fishes such as herring which migrate into estuaries for spawning may also be exposed to environmental extremes, particularly to changes in salinity, which produce additional stress. Further, since aromatics are highly lipid-soluble, it might be expected that benzene would accumulate to high levels in ovarian eggs. These factors could lead to significant reductions in fecundity and serious consequences for populations over long chronic exposures.

The purpose of this experiment was to examine the effect of benzene on female Pacific herring, *Clupea harengus pallasi* Valenciennes, just prior to spawning. We have also studied benzene effects on other life history stages of the herring (Struhsaker et al. 1974; Korn et al. see footnote 2;

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[1] Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, 3150 Paradise Drive, Tiburon, CA 94920.

[2] Korn, S., N. Hirsch, and J. W. Struhsaker. 1976. The uptake, distribution, and depuration of ^{14}C-benzene and ^{14}C-toluene in Pacific herring (*Clupea pallasi*). Unpubl. manuscr.

Manuscript accepted September 1976.
FISHERY BULLETIN: VOL. 75, NO. 1, 1977.

Eldridge et al.[3]). So far as we know, there is no similar study, exposing fish just prior to spawning, for any oil component.

Benzene was selected for most of our studies on herring because of its relatively high proportion in the water-soluble fraction of crude oil and refined products (Anderson et al. 1974), high solubility in water and relative toxicity (Benville and Korn 1974, footnote 4; Korn, Struhsaker, and Benville 1976). Monoaromatics were tested individually rather than exposing fishes to the total oil or total water-soluble fraction in order to more specifically delineate physiological responses to a known toxic component.

Initial research on Pacific herring adults, eggs, and larvae was conducted with high (ppm level) concentrations of benzene (Struhsaker et al. 1974; Korn, Struhsaker, and Benville 1976). Because of the high volatility of benzene, such concentrations would probably occur only briefly after catastrophic incidents, such as tanker accidents and well blowouts. Subsequently, we tested levels in the low ppb (parts per billion) range as being more representative of chronic exposures and potentially more damaging over a long period to marine populations.

In this study, ripe male and female herring were exposed just prior to spawning to 100 nl/liter (ppb) and 800 nl/liter (ppb) benzene for 48 h. The ^{14}C-labeled benzene and its metabolites were measured in the ovaries to determine uptake, accumulation, and depuration. Exposure effects on behavior, the mortality of eggs in the gonads of females, and rate of delayed mortality in embryos at hatching and larvae through yolk absorption were also recorded.

METHODS

Pacific herring were captured 4 December 1974 during the spawning season in San Francisco Bay by a local bait dealer. The fish were captured with a lampara net and wet-brailed from the net into the vessel bait wells. The fish were transported immediately in the bait vessel to the Tiburon Laboratory dock and then transferred to 1,900-liter tanks in the laboratory. Fish were "running ripe" when captured. Because the purpose of these experiments was to expose fish prior to spawning, an acclimation period of only 24 h was allowed. Previous experience with ripe herring has shown that they usually spawn shortly after capture.

Fish were initially placed in circular tanks with double sand-filtered, open flow seawater at ambient conditions in the bay at the time. Initial handling mortality was negligible. During the experiment, conditions were as follows: salinity, 23.0-24.0‰; temperature, 10.0°-11.5°C; oxygen, 6.0-10.5 ppm. An ambient benzene concentration was undetectable at the ppb level. Since herring generally feed poorly when spawning, neither exposed nor control fish were fed during the experiment. The exposure treatments were as follows:

Control: 0 nl/liter (ppb) benzene; open flow system, no benzene exposure; approximately 100 fish (50 males, 50 females).

Exposed: 800 nl/liter (ppb) benzene, open flow system, constant exposure for 48 h; approximately 100 fish (50 males, 50 females).

Exposed: 100 nl/liter (ppb) ^{14}C-labeled benzene; static system, declining exposure, 48 h; 25 females only; linear decrease in benzene concentration to approximately 10% of initial concentration remaining at end of 48 h.

All benzene exposures were terminated and open flow reestablished in the 100 ppb static exposure tank at the end of 48 h. The static exposure of ^{14}C-labeled benzene was to determine the uptake, accumulation, and depuration of benzene in the gonads of females. The open flow constant exposure and control were primarily to establish morphological and mortality effects on the ovarian eggs and delayed effects on subsequent larval development and mortality.

The behavior of fish was observed before sampling. Subsamples of females were taken daily for 6 days—2 days during exposure and 4 days after. Fish were removed randomly until 10 females were obtained from the control and 800 ppb exposure conditions. Five females were removed daily from the static 100 ppb exposure. Concentrations of benzene in the water of all tanks were also measured daily.

Each female sampled was measured (standard length), weighed (wet weight), and the ovaries dissected out. The ovaries were also measured (total length) and weighed (wet weight); the left ovaries were examined microscopically, the right ovaries prepared for radiometric or gas chromatograph analyses. Methods of preparation for radiometric and chromatograph measurements are described elsewhere (Benville and Korn 1974; Korn, Hirsch, and Struhsaker 1976, see footnote 2). It should be emphasized that the radiometric technique measures total radioactivity and concentrations calculated may include metabolites of benzene as well as benzene itself.

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[3] Eldridge, M. B., T. Echeverria, and J. W. Struhsaker. Manuscr. in prep. The effect of benzene on the energetics of Pacific herring (*Clupea harengus pallasi*) embryos and larvae.

[4] Benville, P., Jr., and S. Korn. Manuscr. in prep. The acute toxicity of six mono-cyclic aromatics to striped bass (*Morone saxatilis*) and bay shrimp (*Crago* sp.).

Ovaries were examined under a dissecting microscope for developmental stage [Hjort's stage (Bowers and Holliday 1961)] and the presence of opaque dead or dying eggs, and the gross appearance (color and degree of deliquescence) was ranked. The maximum diameters of 10 eggs from the ovary of each female were measured and the eggs examined for abnormal development.

On day 3, after cessation of exposure, pieces of clean plastic screening were placed around the standpipe in the center of the 800 ppb and 100 ppb exposure and control tanks to provide substrate for spawned eggs. Males were placed with females in the 100 ppb tank. After spawning occurred, the screens were removed and eggs examined for developmental stage and mortality. Pieces of screen with 75 eggs on each (most in 4-cell stage) were cut apart. Pieces of screen were selected with a single layer of relatively separated eggs because previous experience showed reduced survival in dense egg clusters. Two pieces of screen with 75 eggs each were placed in each 8-liter rearing container (total of 150 eggs). There were five replicate containers for each treatment and control (total of 15 containers). Temperature during development was 11.0°-12.0°C, and salinity, 22.0‰. Other rearing conditions were as previously described (Struhsaker et al. 1974). Hatching occurred 10 days after fertilization, and percent survival at hatching was determined from three replicate counts of swimming larvae in each container and by counting the number of dead and abnormal embryos left on the screen. The screens were removed and surviving larvae fed the rotifer, *Brachionus plicatilis*, through the remainder of the experiment (past yolk absorption to larval day 7). Surviving larvae were counted and the percent survival through yolk absorption determined from the original egg number.

Data were analyzed, depending upon variables, with the methods of analysis of variance and covariance using University of California Biomedical programs, BMD 01V, 02V, and 03V (Dixon 1970).

RESULTS

No adult mortalities occurred during the 6 days of the experiment. Stress behavior was noted in exposed fish, particularly at the constant 800 ppb exposure. Definite distress was observed by the end of the first day, although oxygen levels were above saturation. Milling was disrupted, fish were gaping at the surface, and many exhibited disequilibrium. Even after cessation of exposure, stress behavior continued for the duration of the experiment. Control fish may also have been stressed by the capture conditions and the short acclimation period, but they exhibited none of the stress symptoms of exposed fish and milled normally.

Although behavior was abnormal in exposed fish, spawning occurred in the tanks. In fact, the stress from benzene exposure appeared to prematurely induce spawning. This is illustrated in Table 1 by the percentage of exposed fish which were spent (Stage VII) compared with control fish. At the end of the 6-day experimental period, 73% (100 ppb) and 70% (800 ppb) of the exposed fish were spent, compared with only 25% of the controls. The higher percentage of spent females in the 100 ppb static treatment than in the 800 ppb open flow treatment during the first 4 days may be a result of additional stress imposed by static conditions. At all treatments, most unspent ovaries were ripe (Stage VI); only 7-10% were immature (Stages III-V) (Table 1).

No changes in growth (as indicated by wet weight and length) were expected in females over the short experimental period. However, these measurements were taken to determine the similarity of fish between the treatments and to adjust effect of size on the differences in weights of ovaries between the treatments. Ovary length and weight and egg diameters were measured to determine if benzene uptake affected the growth or resorption of ovaries or eggs and to determine the ripeness or proximity to spawning. Data are summarized in Table 2. Egg diameter did not correlate with any other measurement variable. Analysis of variance revealed no significant difference ($P > 0.25$) in egg diameter between 0 and 800 ppb benzene treatments. Since the size range of females varied somewhat between the two treatments (Table 2), analysis of covariance was used to compare the weights of females and ovaries between concentrations and days after adjustment for the effect of lengths (Table 3). No

TABLE 1.—Effects of benzene exposure on ovaries and eggs of Pacific herring.

Hours (Days)	Benzene concentration (nl/l; ppb)	No. of ovaries examined	Percent of eggs in stage[1] III-V Immature	VI Ripe	VII Spent	No. of ripe ovaries examined	Stages III-VI dead eggs No.	%
24	0	10	10	80	10	9	0	0
(1)	100	5	0	40	60	2	0	0
	800	9	40	49	11	8	0	0
48	0	10	0	90	10	9	0	0
(2)	100	5	0	20	80	1	1	100
	800	10	10	60	30	7	1	14
72	0	10	20	70	10	9	0	0
(3)	100	5	20	40	40	2	2	100
	800	9	0	56	44	6	6	100
96	0	10	0	70	30	7	1	14
(4)	100	5	20	20	60	1	1	100
	800	10	10	57	33	6	6	100
120	0	10	10	40	50	5	0	0
(5)	100	5	0	0	100	0-All spent	—	—
	800	9	0	0	100	0-All spent	—	—
148	0	10	0	60	40	6	0	0
(6)	100	5	0	0	100	0-All spent	—	—
	800	10	0	0	100	0-All spent	—	—
Totals	0	60	7	68	25	36	1	3
(6 days)	100	30	7	20	73	6	4	67
	800	57	10	20	70	24	13	54

[1] Hjort's stage: Bowers and Holliday (1961)

TABLE 2.—Mean and range of female standard length, wet weight; ovary length and wet weight; and maximum egg diameter for Pacific herring. Linear equation describes the regression of wet weights on lengths for both whole female fish and left ovaries. Sample size = 59 females; 59 ovaries (spent females excluded).

	Female				Ovary (Stages III-VI)					
	Standard length (X)		Wet weight (Y)		Total length (X)		Wet weight (Y)		Max egg diameter	
Benzene concentration (ppb)	Range (cm)	Mean (cm)	Range (g)	Mean (g)	Range (cm)	Mean (cm)	Range (g)	Mean (g)	Range (mm)	Mean (mm)
0	16.8-22.4	19.3	76.8-239.6	136.8	7.7-11.5	10.4	6.7-30.8	18.2	1.20-1.50	1.30
800	16.4-21.5	18.7	75.3-189.6	120.3	7.5-14.3	9.3	6.3-26.5	13.6	1.20-1.56	1.30
Total	16.4-22.4	19.0	75.3-239.6	126.2	7.5-14.3	9.9	6.3-30.8	15.9	1.20-1.56	1.30
	Regressions[1]									
0	$\hat{Y} = -339.96 + 24.98X$				$\hat{Y} = -19.26 + 3.56X$					
800	$\hat{Y} = -267.50 + 20.89X$				$\hat{Y} = -12.84 + 2.90X$					

[1] Tests of significance between slopes (*b*) and elevations (*a*) of regressions showed no significant difference ($0.100 < P < 0.250$) between concentrations (Snedecor and Cochran 1967:432-436).

TABLE 3.—Analysis of covariance of wet weight on standard length of female, wet weight of ovary on wet weight of female, and wet weight on total length of ovary for Pacific herring. Analysis of ripe ovaries (Stage VI) only. Treatments: Concentrations (0 vs. 800 ppb); Days (1 to 4); 2×4=8 treatment combinations × 5 observations per treatment combination = 40.

Analysis of dependent variable (wet wt female) after adjustment for covariate (standard length female)

Source of variation	df	SS	MS	*F* ratio[1]	Probability	
Between concentrations (C) (0 vs. 800 ppb)	1	5.2508	5.2508	0.24	$P > 0.250$	NS[2]
Between days (D)	3	675.2346	225.0783	1.04	$P > 0.250$	NS
Interaction (CD)	3	485.9035	161.9678	0.75	$P > 0.250$	NS
Within cells	31	6,721.2742	216.8153			

Analysis of dependent variable (wet wt ovary) after adjustment for covariate (wet wt female)

Source of variation	df	SS	MS	*F* ratio	Probability	
Between concentrations (C) (0 vs. 800 ppb)	1	0.6940	0.6940	0.13	$P > 0.250$	NS
Between days (D)	3	2.5351	0.8450	0.16	$P > 0.250$	NS
Interaction (CD)	3	19.4057	6.4686	1.21	$P > 0.250$	NS
Within cells	31	165.5181	5.3393			

Analysis of dependent variable (wet wt ovary) after adjustment for covariate (total length ovary)

Source of variation	df	SS	MS	*F* ratio	Probability	
Between concentrations (C) (0 vs. 800 ppb)	1	0.4585	0.4585	0.04	$P > 0.250$	NS
Between days (D)	3	27.2532	9.0844	0.71	$P > 0.250$	NS
Interaction (CD)	3	8.0860	2.6953	0.21	$P > 0.250$	NS
Within cells	31	398.2616	12.8471			

[1] $F\ 0.05 = 4.16$, df = 1,31; $F\ 0.05 = 2.91$, df = 3,31.

[2] NS = not significant

significant difference ($P>0.25$) between concentrations or days or interaction was found. Tests between slopes (b) and elevations (a) of the regression lines of weights on lengths of females and weights on lengths of ovaries (Snedecor and Cochran 1967:432-436) showed no significant differences ($P>0.10$) between 0 and 800 ppb concentrations (Table 2).

Microscopic examination of the ovaries, however, revealed the presence of dead eggs in ovaries of exposed fish by the second day of exposure (Table 1). No dead eggs were found in control fish until day 4, and then only a few (15-20 eggs) in one female, the rest of the ovary appearing normal. Ovaries of exposed fish contained significantly larger numbers of opaque dead eggs (more than 10%) and were generally paler yellow and deliquescent. By the end of 6 days, 67% (100 ppb) and 54% (800 ppb) of exposed females were found with ovaries containing dead or dying eggs.

The uptake and depuration of benzene in ovaries of females exposed to a static initial concentration of 100 nl/liter (ppb) ^{14}C-labeled benzene is shown in Figure 1, together with data determined from other larval studies for later stages (Eldridge, Struhsaker, and Echeverria[5]). Uptake was rapid, so that a maximum accumulation (1.4 μl/g; ppm) was reached in 24 h. This level was maintained through the 48-h exposure period. After open flow was reestablished and exposure ended, benzene and/or metabolites were depurated until they reached an undetectable level in 96 h. The figure shows that levels accumulated in ovarian eggs were higher and sustained longer than in later egg and larval stages from other experiments with comparable exposure conditions.

Results of rearing experiments with eggs from females exposed to 0 and 800 ppb unlabeled benzene are summarized in Tables 4 and 5. Survival was also reduced in eggs and larvae from females exposed to an initial concentration of 100 ppb labeled benzene. However, results were obscured by an additional variable. Eggs taken from the static exposure tank were covered by filamentous bacterial growth early in development and many eggs died as a result. In the other treatment with open flow and in controls, eggs did not undergo this mortality due to epifloral growth. The 100 ppb treatment, therefore, was not included in the analysis. Analysis of variance showed survival at hatching and survival of larvae through yolk absorption were significantly less in exposed eggs (800 ppb) than in control eggs ($P<0.1$; Table 5). Exposure to ppb benzene levels for only 48 h reduced survival by about 43% through yolk absorption to larval day 7 (Table 4).

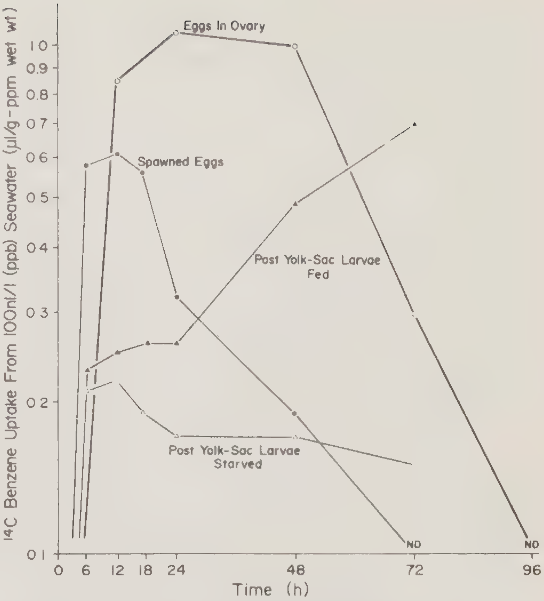

FIGURE 1.—Accumulation of ^{14}C-labeled benzene in different early Pacific herring developmental stages exposed to an initial concentration of 100 nl/liter (ppb) in a static system. Concentrations shown on y-axis were calculated from total radioactivity and may include metabolites derived from benzene as well as benzene. Spawned eggs were in a stage just prior to blastopore closure; post yolk-sac larvae were fed the rotifer, *Brachionus plicatilis*, containing high accumulated levels of labeled benzene. ND = not detectable.

DISCUSSION

When female herring were briefly exposed to low levels of benzene for 48 h just prior to spawning, a significant reduction occurred in survival of eggs and resultant larvae from the ovary through yolk absorption. It is probable that further mortality would have occurred in later larval stages if the experiments were continued. When this result is compared with that from exposing other life history stages after spawning (Struhsaker et al. 1974; Eldridge et al. see footnote 5) where survival is not affected except at ppm levels, it appears that the spawning female and ovarian eggs are the most sensitive stages.

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[5] Eldridge, M. B., J. W. Struhsaker, and T. Echeverria. Manuscr. in prep. The uptake, accumulation and depuration of ^{14}C-labeled benzene in embryos and larvae of Pacific herring (*Clupea harengus pallasi*).

TABLE 4.—Mean percent survival through hatching and yolk absorption of Pacific herring larvae from eggs of benzene-exposed and control females.

Stage	Benzene concentration (nl/l; ppb)	Total no. of eggs	Mean survival (%)	95% confidence interval (%)	Mean reduction survival[1] (%)
Embryos to hatching	0	750	92.9	91.5-94.3	
	800	750	66.6	64.1-69.1	-26.3
Hatched larvae through yolk absorption	0	750	76.7	74.5-78.9	
	800	750	34.4	32.0-36.8	43.3

[1] See Table 5 for test of significance

TABLE 5.—One-way analysis of variance in survival of Pacific herring embryos to hatching and larvae through yolk absorption (larval day 7). Ripe females exposed prior to spawning. Five replicate containers per treatment; 150 eggs/container. (Arcsin transformation applied to percent survival data.)

Percent survival to hatching

Source of variation	df	SS	MS	*F* ratio	Probability
Between concentrations 0 vs. 800 ppb	2	1.3442	0.6721	95.6098**	$P<0.01$
Within groups	12	0.0843	0.0070		
Total	14	1.4285			

Percent survival through yolk absorption

Source of variation	df	SS	MS	*F* ratio	Probability
Between concentrations 0 vs. 800 ppb	2	0.8053	0.4026	30.2147*	$P<0.05$
Within groups	12	0.1599	0.0133		
Total	14	0.9652			

Although male herring were not studied in detail here, their behavior was severely disrupted, as in the females. Testes of mature, spawning herring have been found to contain higher levels of cholesterol (a lipid) during spawning than at other times in their adult life (Blaxter and Holliday 1963), and it is possible the lipid-soluble benzene may accumulate to high levels in testes of ripe males. Effects on males and their spermatozoa, as well as effects on females, may have contributed to reduction in survival of fertilized eggs through yolk absorption in these experiments.

Reference to Figure 1 shows that the maximum accumulation of labeled benzene in ovarian eggs was greater than in later egg and larval stages as measured in other experiments. Accumulation in ovarian eggs of exposed females was approximately twice that in eggs exposed just after spawning and prior to blastopore closure and about six times that in embryos exposed just after yolk-sac absorption. Accumulation for the first 48 h of water column exposure in these stages appears to correlate with the yolk volume of the eggs and larvae, decreasing as yolk is utilized, as would be expected with lipid-soluble benzene. However, the decreased accumulation may also relate to the development of enzymes enabling later stages to metabolize benzene and subsequently depurate more rapidly. After being fed *Brachionus plicatilis*, which accumulate high levels of benzene (Echeverria[6]), the fish larvae rapidly accumulated benzene from their food (Figure 1). Other studies of accumulation in tissues of adult herring (Korn et al. see footnote 2) show that only one site, the gall bladder with bile, accumulates higher concentrations than ovarian eggs (30 times and 14 times initial concentration, respectively).

I have noted previously (Struhsaker et al. 1974) that the percentage survival of eggs through hatching is significantly less (approximately 25% less; $P<0.01$) in Pacific herring eggs collected from San Francisco Bay than in those from Tomales Bay. Although other environmental differences may be involved, this reduction in hatching success may well relate to the effects of accumulated pollutants in the gonads of spawning fish in the relatively more polluted San Francisco Bay waters and warrants further study.

Estimating that the reduction in survival of eggs through yolk absorption of spawning exposed females is at least 43%, the effect on Pacific herring populations exposed to only one toxic component of petroleum could be significant. Considering that the total water-soluble fraction contains many other toxic aromatics, it is possible that long-term chronic exposures to low levels may be decreasing population survival in polluted areas. In addition, chlorinated hydrocarbons in pesticides may also be accumulating in the gonadal lipids and interacting with petroleum hydrocarbons producing even more deleterious effects. More studies of the effects of these components on spawning fish are clearly needed. If fishes prove generally to be the most sensitive to accumulated oil components during their spawning season, fisheries management decisions should take into consideration their protection from damaging levels, particularly at spawning time.

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[6] Echeverria, T. Manuscr. in prep. Uptake and depuration of ^{14}C benzene in the rotifer, *Brachionus plicatilis*.

ACKNOWLEDGMENTS

I thank the staff of the Physiology Program, SWFC Tiburon Laboratory, for assisting me in these experiments. I am grateful to Norman Abramson and Vance E. McClure for reviewing the manuscript and for making suggestions. Dale Straughan, Institute of Marine and Coastal Studies, University of Southern California, also reviewed the manuscript and made several improvements.

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The Fishery for Nehu, *Stolephorus purpureus*, a Live Bait Used for Skipjack Tuna, *Katsuwonus pelamis*, Fishing in Hawaii

RICHARD N. UCHIDA[1]

ABSTRACT

With increasing interest in the baitfish resources and their capacity to support local skipjack tuna, *Katsuwonus pelamis*, fisheries, we need to evaluate their distribution and relative abundance. This paper describes the trends in production of nehu, *Stolephorus purpureus*, an anchovy used as live bait in the fishery for skipjack tuna in Hawaiian waters.

Kaneohe Bay and Pearl Harbor, two of the most important baiting sites in the Hawaiian Islands, produce 71% of the bait. Another important site on Oahu, particularly for night baiting, is Kalihi-Keehi Lagoon.

Day baiting produced 79% whereas night baiting produced 21% of the State's nehu catch. Catches and baiting effort showed a downward trend in the day fishery and an upward trend in the night fishery in 1961-65. In 1966-72, however, catches and baiting effort increased steadily in the day fishery whereas they declined in the night fishery.

INTRODUCTION

The Hawaiian pole-and-line fishery for skipjack tuna, *Katsuwonus pelamis*, is dependent on a steady supply of live bait. Essentially, two separate fisheries are involved. The first is for live bait which is caught with nets in shallow waters of bays and harbors. The second is for skipjack tuna and other tunas which are caught in offshore waters with pole and line after the fish are attracted to the boat with live bait. Thus, live bait is essential in the Hawaiian skipjack tuna fishery, and fishermen spend a good part of their time catching it. This report presents and analyzes the bait catch statistics associated with the Hawaiian skipjack tuna fishery for the years 1960 to 1972. It supplements a previous report on the Hawaiian skipjack tuna fishery by Yamashita (1958).

SPECIES UTILIZED

Basically, almost any small fish in sufficient numbers can be used as live bait, but their effectiveness varies from species to species. By far, Hawaiian skipjack tuna fishermen prefer the nehu, *Stolephorus purpureus*, a small (40-60 mm), fragile anchovy that schools over sand and mud bottoms in harbors and bays throughout the Hawaiian Islands. It apparently possesses most of the qualities of a good baitfish. Captured both day and night, nehu constitutes roughly 97% of the bait caught in Hawaiian waters. Most of the remainder is made up of silverside or iao, *Pranesus pinguis*, and small round herring or piha, *Spratelloides delicatulus*.

BAITING LOCALITIES

Within the Hawaiian Islands there are several baiting grounds; they are listed below, by islands.

Island	*Baiting grounds*
Oahu	Kaneohe Bay
	Pearl Harbor
	Kalihi-Keehi Lagoon
	Honolulu Harbor
	Ala Wai Canal
	Kewalo Basin
	Waialua Bay including Haleiwa
Maui	Maalaea Bay region including Kihei
	Lahaina
	Kahului including NASKA (formerly Naval Air Station, Kahului)
Hawaii	Hilo Harbor
	Kawaihae
	Mahukona
	Kailua-Kona
Kauai	Port Allen
	Hanalei
	Nawiliwili
	Hanapepe
Molokai	Kaunakakai
Lanai	—

Oahu has the most important bait resource. Roughly 79% of the State's bait production comes from Oahu's baiting grounds (Fig. 1). Two of them, Kaneohe Bay on the windward side and Pearl Harbor on the leeward side of Oahu, are the major sources of bait, providing about

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[1] Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

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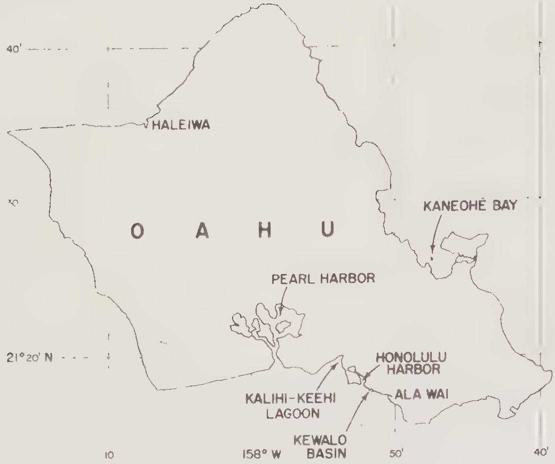


Figure 1.—Baiting areas on Oahu.

71% of the State's production. A third site of some importance, particularly for night baiting, is Kalihi-Keehi Lagoon. Generally, Oahu-based vessels do their "baiting" (catching of bait) on Oahu although they may also bait at Kauai, Maui, Molokai, and Lanai. Maui-based vessels usually bait on Maui, Oahu, Molokai, and Lanai, but rarely venture to Kauai. Hawaii-based vessels are generally restricted to grounds off their island. They capture a large proportion of their live bait at night as Hilo Harbor is fringed by a predominantly rocky shoreline that is not suitable for day seining.

METHODS OF CAPTURE

Bait is caught by two methods in the Hawaiian Islands. Day baiting usually starts at dawn and ends when enough bait for a day's fishing has been caught. If day baiting is unproductive, night baiting is attempted and, if little or no night bait is caught, day baiting is resumed the next morning.

Day Baiting

Day baiting may last for 1.5 to 7 h but usually lasts about 3 h (Uchida and Sumida 1971). The fishermen use an outboard-powered skiff loaded with a surround net measuring roughly 156 m (80 fathoms) long and 7 m (4 fathoms) deep (June 1951). They scout the shallow waters of bays and harbors. When a school of baitfish is located, the net is set from the skiff as the skiff encircles the school. The net is then partially "dried up" to form a bag to hold the school. To keep mortalities to a minimum, the fishermen "swim" the net-enclosed baitfish to the vessel. Once alongside the vessel, the fishermen, using 23-liter capacity (about 6 gal) stainless steel buckets, brail the fish from the net into the baitwells. Each scoop of the bucket contains both water and baitfish to minimize injury to the baitfish. The amount of baitfish in a bucket varies considerably. Yamashita (1958) estimated the amount of nehu in a bucket to be about 3.2 kg (7 lb), but recent estimates (Hida and Wetherall 1977) indicate that the actual weight of the baitfish in a bucket may be about 22-24 kg (10-11 lb). Usually, several sets are required to obtain enough bait to justify tuna fishing. Uchida and Sumida (1971) estimated from data collected in June-August 1967 that the average is about three sets although as many as nine sets in a single day may not be uncommon.

Night Baiting

For night baiting, lift nets which measure about 27-46 m (15-25 fathoms) long and 22 m (12 fathoms) deep are used (June 1951). Night baiting does not involve active scouting for schools of baitfish. Rather, a submerged light is used to take advantage of the fact that nehu are attracted to light. After dark, the vessel is anchored or moored and a light is suspended several feet below the water surface from a 6-m (20-ft) pole which is lashed to the vessel's portside. Just before daybreak, a rheostat dims the light causing the baitfish to concentrate. The net is set around the tightly schooled baitfish from a skiff and the captured bait is transferred to the baitwells. Uchida and Sumida (1971) found that night-baiting operations from setting the light to drying up the net, usually lasted 8 h. Usually one set is made per night.

CATCH, EFFORT, AND CATCH PER EFFORT

The bait reports, turned in by the fishermen to the Hawaii Division of Fish and Game, were summarized by baiting locality and by time of baiting (day or night). Reports which showed nehu catches but gave no indication of day or night baiting, and those which indicated the capture of baitfish other than nehu, were included only in statewide summaries. In the following sections, I discuss bait production in the day and night fisheries.

STATEWIDE PRODUCTION

Statewide catch statistics of baitfish, combined for all species, baiting grounds, and times of capture, are plotted in Figure 2. With the exception of 1960, when the baitfish catch amounted to 22,849 buckets, catches in 1961-72 have never fallen below 30,000 buckets annually and in some years they have been well over 35,000 buckets. The peak in bait production occurred in 1971 when 42,098 buckets were caught.

Baiting effort tended to drift upward in 1960-65 and downward in 1966-72. Actually the uncorrected effort presented in Figure 2 includes both day and night effort and does not take into account the curtailment of night-baiting operations after 1965 concurrent with increases in day-baiting operations. As I will discuss in later sections, 1 day of baiting will usually produce a catch which is much greater than that obtained by night baiting. The

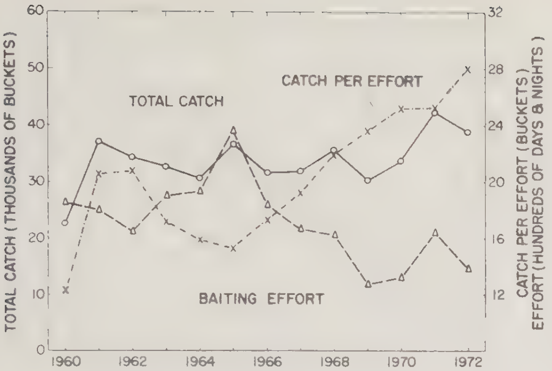


Figure 2.—Catch, baiting effort, and catch per effort in the fishery for live bait in Hawaii, 1960-72.

progressive increase in catch per effort in 1965-72, therefore, results from an increase in day baiting and a decrease in night baiting.

DAY-BAIT PRODUCTION

The statewide production of day bait averaged 25,338 buckets in 1960-72. In 1960, production reached 15,735 buckets with 1,001 days of baiting effort. Figure 3A shows that although production rose in 1961, day effort started on a downward trend that also carried production to lower levels. An upturn in production occurred in 1965, but day effort did not begin its upward climb until 1968, when it reached 1,055 days. The result was that production climbed to 30,148 buckets. Poor tuna fishing in 1969 dropped baiting intensity to 870 days and production to 25,650 buckets. In 1970, an upward trend started that was to carry day effort well over 1,000 days and production to exceptionally high levels, particularly in 1971 when 1,334 days of baiting produced 38,786 buckets.

In terms of apparent abundance, as measured by catch per day baited (C/D), only 15.7 buckets/day were taken in 1960 (Fig. 3A). The C/D rose sharply thereafter to 28.6 buckets in 1962, then declined to 23.8 buckets in 1964-65. In 1966-67, however, an upswing occurred and in recent years, catches have been nearly 30 buckets/day. The peak in the index was reached in 1972 when 31.2 buckets of bait were caught per day's baiting. The overall average for the 13-yr period was 27.1 buckets/day of baiting.

Among the State's baiting grounds, Pearl Harbor was the most productive for day-baiting operations. In general, both bait production and baiting intensity at Pearl Harbor show an upward trend (Fig. 3B). Production averaged 10,127 buckets annually and accounted for 40% of the statewide average catches. Annual catches ranged from a low of 3,517 buckets in 1960 to a high in 1971 of 18,992 buckets.

Day effort expended at Pearl Harbor paralleled the annual catches. It ranged from a low of 244 days in 1962 to a high of 687 days in 1971. The average over 13 yr was 396 days or roughly 42% of the average annual day-baiting effort statewide.

The abundance index for Pearl Harbor showed very little variation and no distinct trend over the years (Fig. 3B). Abundance was lowest in 1960 when only 13.5 buckets/day were caught. The indices in 1961-72 fluctuated within a fairly narrow range between 23.4 and 28.1 buckets. The average C/D in 13 yr was 25.6 buckets.

Kaneohe Bay, the second major ground for day bait, produced an average annual catch of 8,783 buckets of nehu. This catch represented about 35% of the day bait caught annually in the State. The annual catches tended to decline in 1960-64 (Fig. 3C). But the upward trend which started in 1965 carried production to well over 10,000 buckets in 1966-72. Production, at a low of 2,116 buckets in 1964, increased over sevenfold to a peak of 15,709 buckets in 1970.

The effort expended in day baiting at Kaneohe Bay also varied widely. The progressive decline in baiting intensity in 1960-64 was reversed in 1965-72 (Fig. 3C). The low production in 1964 resulted from baiting effort of only 69 baiting days whereas the high production of 1970 resulted from expending 418 days on baiting. Over the 13-yr period, an average of 253 baiting days were expended at Kaneohe Bay, representing 27% of the statewide day-baiting effort.

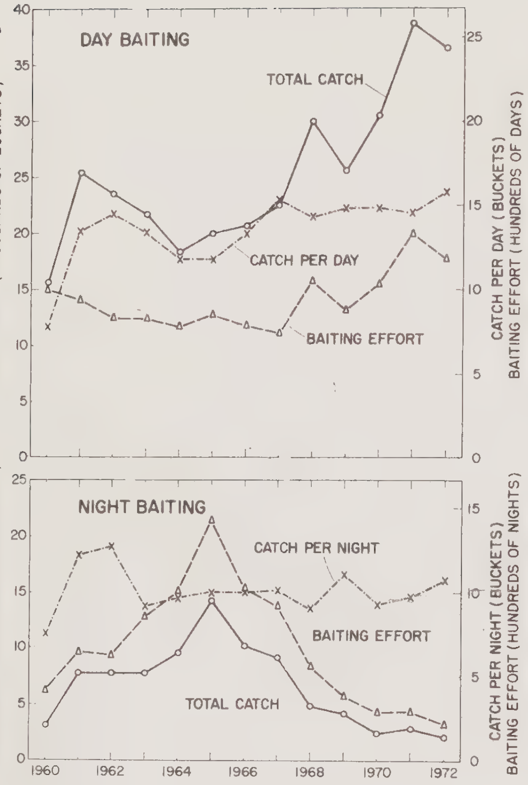
The apparent abundance of nehu at Kaneohe Bay was lowest in 1960 when only 17.3 buckets/day were taken. The abundance index in the following year increased to 28.7 buckets and has not fallen below this level since (Fig. 3C). An estimate of 43.3 buckets/day in 1972 was the highest level attained by the index. The 1960-72 average was 34.7 buckets/day. This was roughly a third higher than the average calculated for Pearl Harbor.

Catches of day bait from Kalihi-Keehi Lagoon and Honolulu Harbor were small. Kalihi-Keehi Lagoon had an annual production which averaged 968 buckets and represented about 4% of the statewide day-bait catches. Both the catches and baiting effort in the day fisheries showed a downward trend (Fig. 3D). Day catches from Honolulu Harbor averaged 259 buckets/yr and accounted for only about 1% of the State's total. Catch and day-baiting effort fluctuated widely over the years but the trend in these indices was upward (Fig. 3E). From all other baiting areas, summarized under "Other Areas," production averaged 5,200 buckets/yr and represented about 20% of the State's production. The trend in catch and day-baiting effort was downward in 1961-67 and upward in 1968-72 (Fig. 3F).

NIGHT-BAIT PRODUCTION

From the annual catch statistics for night bait, it is evident that the catches, plotted over the years 1960-72, follow a bell-shaped curve with relatively low production in 1960-63, fairly high production in the mid-1960's, and back to low production in 1968-72 (Fig. 3A). Statewide data on night baiting show that in 1960, 3,069 buckets of nehu were caught in 408 nights of baiting. Production and baiting intensity rose to progressively higher levels until 1965 when 1,424 nights of baiting produced a peak catch of 14,251 buckets of nehu. A

A


DAY BAITING
TOTAL CATCH
CATCH PER DAY
BAITING EFFORT
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CATCH PER DAY (BUCKETS)
BAITING EFFORT (HUNDREDS OF DAYS)
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NIGHT BAITING
CATCH PER NIGHT
BAITING EFFORT
TOTAL CATCH
CATCH PER NIGHT (BUCKETS)
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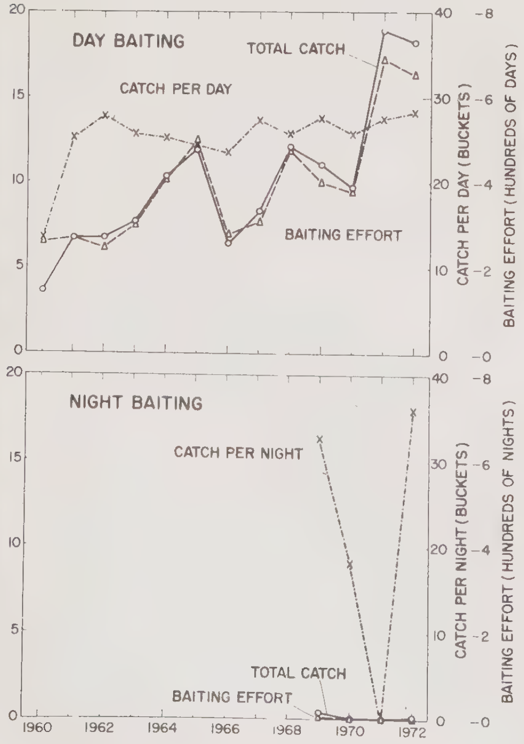
DAY BAITING
TOTAL CATCH
CATCH PER DAY
BAITING EFFORT
TOTAL CATCH (THOUSANDS OF BUCKETS)
CATCH PER DAY (BUCKETS)
BAITING EFFORT (HUNDREDS OF DAYS)
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NIGHT BAITING
CATCH PER NIGHT
TOTAL CATCH
BAITING EFFORT
CATCH PER NIGHT (BUCKETS)
BAITING EFFORT (HUNDREDS OF NIGHTS)
1960
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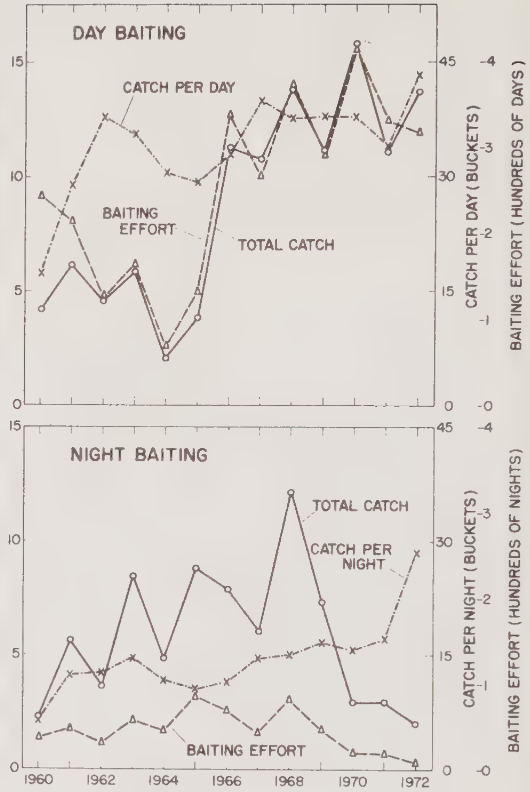
C


DAY BAITING
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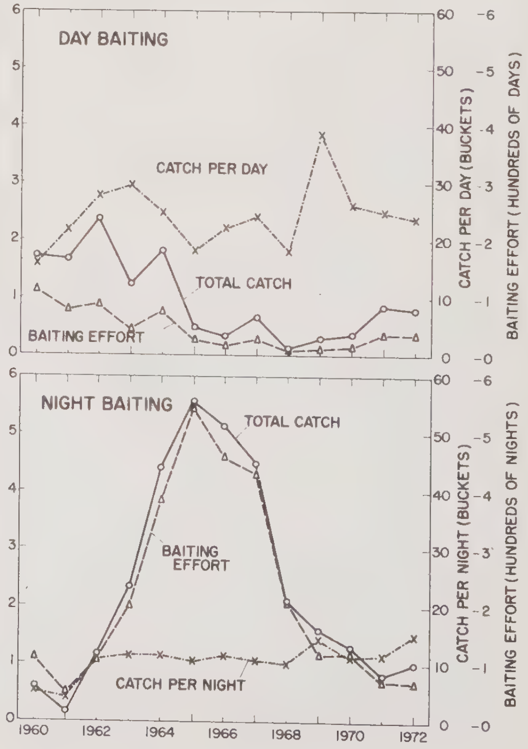
DAY BAITING
CATCH PER DAY
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NIGHT BAITING
TOTAL CATCH
BAITING EFFORT
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CATCH PER NIGHT (BUCKETS)
BAITING EFFORT (HUNDREDS OF NIGHTS)
1960
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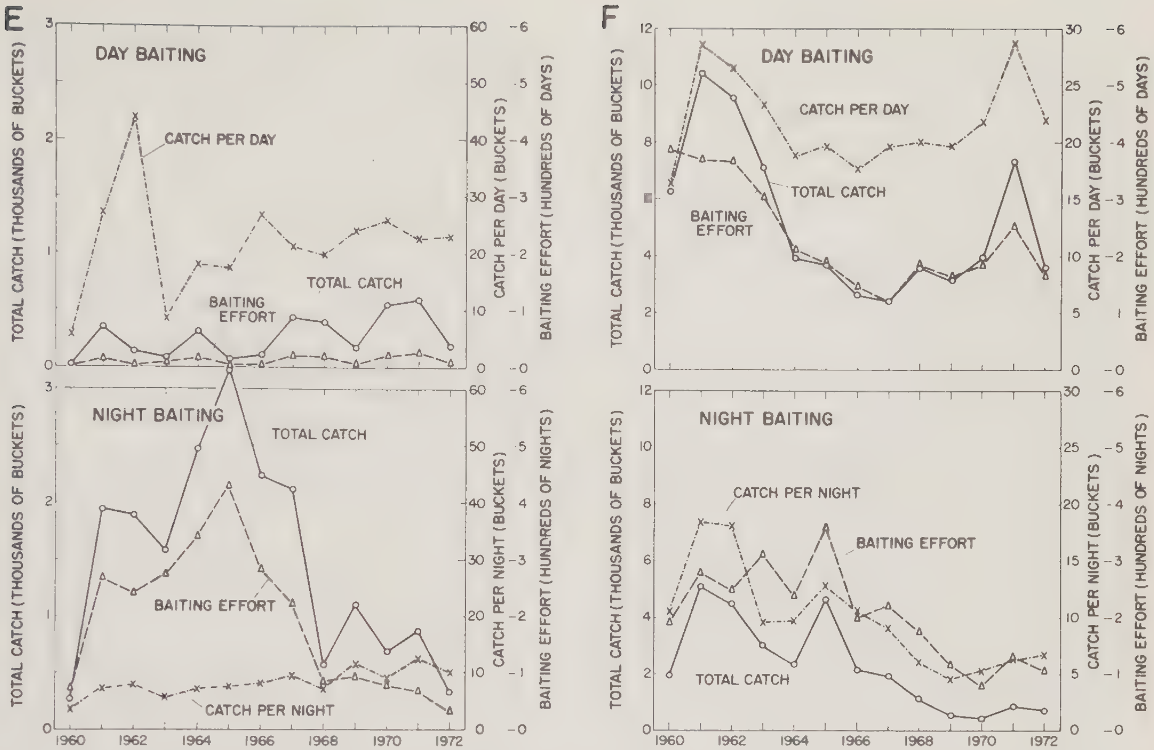

Figure 3.—Catch, baiting effort, and catch per effort in the day and night fisheries for nehu, in Hawaii, 1960-72. A. Total catch in Hawaii, 1960-72. B. Pearl Harbor. C. Kaneohe Bay. D. Kalihi-Keehi Lagoon. E. Honolulu Harbor. F. Other areas in Hawaii.

downward trend in night baiting started the following year and by 1972, only 2,187 buckets were produced in 206 nights of baiting. The average annual production and baiting intensity were 6,648 buckets and 659 nights, respectively.

Among the grounds contributing to night-bait production, Kalihi-Keehi Lagoon was by far the most important. In 1960-65, production rose sharply from a low of 188 buckets in 46 nights of baiting in 1961 to a high of 5,570 buckets in 547 nights in 1965 (Fig. 3D). A decline, starting in 1966, resulting from a change in emphasis to less night baiting and more day baiting, carried production progressively lower in subsequent years. The average annual production, representing about 35% of the statewide night catches, was 2,347 buckets. An average of 220 nights expended at Kalihi-Keehi Lagoon annually accounted for about 33% of the statewide night effort.

Estimates of nehu abundance at Kalihi-Keehi Lagoon were low in 1960-61, falling below six buckets per night in both years (Fig. 3D). Catch per night calculated for 1962-72 was 10 buckets or more and reached a peak of 15.0 buckets in 1972. The average for the 13-yr period was 10.7 buckets.

Second in importance in night-bait production was Honolulu Harbor. The night-bait catch from here was lowest in 1960 when 259 buckets were caught in 72 nights of baiting. An increase in night-baiting intensity in subsequent years was reflected in progressively higher catches. In 1965 the production reached 3,175 buckets, a 12-fold increase (Fig. 3E). A steady decline in night-baiting intensity carried production progressively lower and by 1972, 30 nights devoted to night baiting produced only 303 buckets. The average annual catch was 1,464 buckets representing 22% of the statewide night production. Night effort at Honolulu Harbor amounted to 190 nights or 29% of the statewide night effort.

The abundance of nehu caught per night averaged 7.7 buckets in 1960-72. Whereas the abundance index was 9.5 buckets or less in 1960-68, it was higher in 1969 and in 1971-72. The peak of 12.4 buckets was attained in 1971 (Fig. 3E).

Among the remaining areas, several were relatively good for night baiting. Kaneohe Bay produced an average annual catch of 575 buckets or roughly 9% of the statewide night catches. Grounds at Hawaii and Kauai, included in the statistics for "Other Areas," were also moderately good for night baiting.

SUMMARY

The purpose of this report was to examine the trends in the production of nehu, *Stolephorus purpureus*, a live bait used for skipjack tuna fishing in Hawaiian waters. Briefly, the results showed that nehu constitutes roughly

97% of the bait caught in the Hawaiian Islands. Kaneohe Bay and Pearl Harbor, both of which are important baiting sites on Oahu, produce 71% of the bait. Another important site on Oahu, particularly for night baiting, is Kalihi-Keehi Lagoon.

Statewide, annual bait production in 1960-72 fluctuated between 22,849 and 42,098 buckets and averaged 33,658 buckets. Baiting effort varied from 1,271 days and nights in 1960 to 2,365 days and nights in 1965 and averaged 1,713 days and nights. Catch per effort fluctuated widely from 12.3 buckets in 1960 to 28.0 buckets in 1972 and averaged 19.6 buckets.

Day baiting produced 79% whereas night baiting produced 21% of the State's production. In 1960-72, day-bait production averaged 25,338 buckets, day effort averaged 936 days, and catch per day amounted to 27.1 buckets. The average annual production from night baiting was 6,648 buckets, whereas night effort averaged 659 nights. The catch per night was 10.1 buckets in 1960-72.

In general, catches and baiting effort in the day fishery for nehu showed a downward trend in 1961-65 and an upward trend in 1966-72. On the other hand, catches and baiting effort in the night fishery showed an upward trend from 1960 to 1965 then declined steadily in 1966-72.

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A mathematical model of the relationship between larval anchovy (*Engraulis mordax*) growth, prey microdistribution, and larval behavior

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Keywords:
Anchovy, Larvae, Growth, Microdistribution, Contagion, Behavior, Markov chain, Random walk

Synopsis

A prey concentration dependent random walk model of feeding behavior in larval anchovy based on behavioral experiments was used in conjunction with an experimentally verified Markov chain prey attack rate model to evaluate the relationship between anchovy larval growth from 0.4 to 2.0 cm at various levels of contagion and temperature in the food prey environment. Contagion was regarded as being described by the negative binomial distribution while the actual prey particle size distribution was taken from actual prey particle surveys in areas where anchovy larvae are found. Other important physiological parameters necessary for the construction of the model are taken from existing literature and a description of the complete computer integration of the various submodels presented. Results demonstrate the extreme importance of food microstructure geometry and behavior in the growth rates and growth curves of the anchovy larvae. In particular extremely nonlinear growth rates as functions of contagion are observed in the model with the highest growth rates not occurring at the highest level of prey contagion. The implications these results have in explaining current paradoxes between laboratory-grown larval anchovy prey concentration requirements and those found in the ocean are discussed. Also, the relationship between physical oceanography and larval survival is discussed in light of the results in addition to the need for a more detailed understanding of food prey microstructure in larval ecology.

Introduction

The survival of fish larvae in the open ocean has long been a question of great interest to biological oceanographers for both practical and theoretical reasons. From a practical standpoint this interest stems primarily from the rather inconsistent relationship observed between the size of spawning populations of fish and the size of subsequent year classes. This relationship is believed to exist because of large scale fluctuations in larval mortality due to unassessable changes in predation, food availability, and other important environmental variables affecting larval survival and the effect larval survival ultimately has on recruitment. Thus, the practical importance of larval survival is its relationship to recruitment and how recruitment is variously used in fisheries management. Gulland (1973), however, states that at present, despite the vast amount of laboratory and field work on food chain analysis and its relationship to fish production, no promising and practical method exists to predict adequately recruitment short of vast and costly enterprises extended over long periods of time.

Received 26.7.1976 Accepted 21.2.1977

The theoretical interest in larval fish survival primarily centers on the relationship the young fish have to the whole ecological structure in which they find themselves. In the case of the larval anchovy, an intriguing aspect of such studies has been the apparent discrepancy between the density of appropriate food in the laboratory required for moderate growth and the density of analogous food types in the ocean where anchovy larvae are distributed (Kramer & Zweifel 1970, Lasker et al. 1970, Hunter 1972, 1976, 1977). This discrepancy has led most observers to conclude that rich feeding grounds must exist in the areas where anchovy larvae live which are not adequately detected by current sampling schemes. That is, although the mean densities of food particles observed would not support larval anchovy growth, isolated areas must exist in the sea, despite the mean density estimates, which can very adequately support such growth.

It was this reasoning which led Lasker (1975) to the successful search for such advantageous feeding grounds in the habitats of the larval anchovy and to study the relationship of such habitats to successful first feeding. This work pointed up the importance of more focused analysis on environmental food aggregations and how possible alterations of these aggregations could have important implications for larval survival. Lasker is no doubt correct that such habitats are truly advantageous to first feeding larvae as evidenced by the ability of his laboratory-reared larvae to fill their guts rapidly when placed in water drawn from these regions. However, these rich food areas probably cannot alone completely account for the immense success of the anchovy larvae which support the size of the population believed to exist off the California coast. That is, the blooms of *Gymnodinium* and other phytoplankters found by Lasker (1975), although excellent for first feeding larvae, will not support the young fish to a length exceeding 5.0 mm (Hunter 1977). Therefore, either other appropriate food types are aggregated in the blooms which allow the larvae to continue to grow or young fish can and do survive in other areas where such appropriate food types can exist in sufficient density.

These considerations naturally give rise to the question of the relationship between the amount and geometric distribution of food in the environment of larval anchovies and the animal's growth rate and ultimate survival. However, such questions require for their solution relatively detailed understanding of both the structure of the important environmental parameters on small scales and the behavioral and physiological modifications of the larvae induced by such parameters. Unfortunately, too little is known at the necessary scale about the food structure of the larval anchovy to permit a completely realistic formulation of these relationships. A sufficient amount of information, however, is now available about the changes induced in the behavior and physiology of anchovy larvae 0.4 to 2.0 cm in length by different environmental factors to allow an attempt at such an understanding dependent on building a realistic model of the food microstructure from available data. Such an approach has the advantage of being species specific and of being able to test environmental structures at scales not detected with current sampling schemes. The results obtained can be compared with known laboratory growth studies and provide an insight into the small-scale relationships in the ocean which may have significant consequences for the survival of these organisms and which cannot be assessed with present methods.

It is the purpose of this paper to construct and analyze a model that will simulate dynamically the interrelationship between the anchovy's larval physiology and behavior and its food microdistribution, particularly as they affect larval growth. The model will simulate the growth of the larvae at the beginning of exogenous nutrition from 0.4 cm to the onset of schooling at 2.0 cm for various levels of contagion of food organisms. This range was selected because our knowledge of behavioral and physiological modulations by the environment have only been determined quantitatively for these size ranges. The model will be presented in five sections each dealing with the major components required to construct the complete system. The assumptions underlying each submodel will be discussed and data presented to verify the predictions of the submodels when such data exists. The complete system of submodels and the flow diagram of their interactions will be presented in a final section, and the growth simulations created using the complete system analyzed and discussed. The implications these studies have for larval growth requirements in the ocean and the need for possible alternative investigative methods or approaches to the study of the larval food microenvironment will then be reevaluated in light of the model obtained.

A random walk model of larval anchovy feeding behavior

The foraging behavior of the larval anchovy has been well documented and analyzed (Hunter 1972, Hunter & Thomas 1973) and, in general, is well suited to mathematical modeling. This is primarily because larval anchovy forage behavior can be easily separated into discrete excursion elements in three dimensions (Hunter 1972, Vlymen 1974). Foraging behavior by the larval anchovy is not a purely random three dimensional motion but rather one that within distances comparable to the larval length exhibits only small excursions perpendicular to the previous direction of motion. This allows for the application of a behaviorally-modified three dimensional random walk which models the significant elements of the animal's foraging behavior as observed in the laboratory.

The classical random walk problem in three dimensions effectively seeks to calculate the mean distance traveled after N steps or excursions of fixed length when each subsequent excursion is taken at a random orientation or heading from the preceding (Debye 1946). Casual observation of foraging anchovy larvae may suggest this to be an appropriate description but if such a description was correct it would imply that at each motion the probability of relatively 'behind' excursions i.e., in the opposite direction to the previous excursion, was approximately the same as relatively 'forward' excursions i.e., in the same direction as the previous excursion. For a fish larva which has forward binocular vision and which morphologically is designed for basically forward motions, this seems to be a too unrestricted and unrealistic description. The more likely description of the situation is that forward excursion probabilities are weighted or preferred by the larva with the degree of preference being determined by environmental factors.

This type of behavior was quantitatively elucidated by Hunter & Thomas (1973) who utilized a four direction, two dimensional bounded random walk analysis to investigate the effect of prey distribution and density on the searching and feeding behavior of larval anchovy. They found a distinct preference for 'ahead' motions that were continuously modulated by prey density and which ultimately affected the amount of area searched as calculated by their analysis. That is, high food density tended to equalize the value of each of the four directional probabilities they measured and to decrease the area covered by the anchovy, while low food densities tended to increase the ahead probabilities compared to the other three and to increase the amount of area covered. Hunter & Thomas (1973) felt this behavioral modulation had significant survival implications because it allowed anchovy larvae to remain in areas of high food density longer and thus increase their food ration and ultimate survival.

The data obtained by Hunter & Thomas (1973) suggests that an adequate continuous mathematical description of this behavior could be attained by use of the circular normal distribution. This distribution has had wide application in the study of biological phenomena and a thorough discussion of its use in the biological sciences can be found with relevant bibliography in Batschelet (1965). Using the notations of Batschelet (1965), the density function, $f(\alpha)$, for the circular normal distribution is given by

$$f(\alpha) = \frac{1}{2\pi I_0(k)} e^{k \cos(\alpha - \psi)} \quad , \qquad (1)$$

where ψ is the angle where $f(\alpha)$ takes its maximum value, k is a coefficient of concentration or, as I call it here, the dispersion coefficient (to prevent confusion with particle concentrations later on) and $I_0(k)$ is the modified Bessel function of the first kind. This density function says in effect that the probability of an angle heading by the feeding larval anchovy in the range α to $\alpha + d\alpha$ is given by $f(\alpha)d\alpha$ and is greatest for headings or angle directions in the vicinity of ψ. That is, the circular normal distribution has an inherent central tendency, the degree of which is determined by k, the dispersion coefficient. The analogy to the results of Hunter & Thomas (1973) is now clear and the foraging pattern can be described by a circular normal distribution with a food concentration dependent dispersion coefficient k(c), where c is the food concentration in particles-cm^{-3}. For simplicity and without loss of generality, ψ can be assumed to be zero, as the choice of the coordinate system is arbitrary. Thus, the 'forward' direction will be regarded as having the heading 0, 'left' $\pi/2$, 'behind' π, and 'right' $3\pi/2$ where the directions are in the sense of Hunter & Thomas (1973). Now the description of the foraging behavior as I have reformulated it is as follows. Let an anchovy larva be allowed to execute foraging excursions starting at an arbitrary angle heading θ in a concentration of food particles c. The probability that the ith excursion has a heading between θ_i and $\theta_i + d\theta_i$ is then given by

$$\frac{e^{k(c)\cos\theta_i}}{2\pi I_0(k(c))} d\theta_i \qquad (2)$$

and constitutes the formulation for the heading probabilities that will be used in the subsequent random walk derivation.

The functional relationship k(c) can be found by computing k using the directional probabilities for each concentration of food type as given in Hunter & Thomas (1973). The method used is outlined in Batschelet (1965) and consists of first finding the empirical mean vector which points toward the center of mass of the food concentration data. If we designate the directional probabilities at each concentration of food type by $p_i(c)$ then the components of the mean vector are given by

$$\rho_x(c) = \sum_i p_i(c) \cos\theta_i \quad , \qquad (3)$$

$$\rho_y(c) = \sum_i p_i(c) \sin\theta_i \quad , \qquad (4)$$

where the θ_i, refer to the four directions given above.

The magnitude of ρ is given by

$$\rho\,(c) = \sqrt{\rho_x^2 + \rho_y^2}$$

and for the circular normal distribution this turns out to be related to k in the following manner

$$\rho\,(c) = \frac{I_1(k(c))}{I_0(k(c))} \quad , \tag{5}$$

where $I_1(k(c))$ is the modified Bessel function of the second kind. The results of the above analysis using the data in Hunter & Thomas (1973) are shown in Figure 1 and the least squares fit to the data yields the relation

$$k(c) = 1.47\ c^{-0.247} \quad . \tag{6}$$

This relation has the desired characteristic of a decreasing dispersion coefficient i.e., reducing the tendency to go straight ahead as the food concentration increases.

The anchovy larva's movements may now be regarded as a random walk in three dimensions with a circular normal heading probability distribution which in turn incorporates a food density dependent dispersion coefficient. What is needed is an estimate of the mean square distance traveled, $\langle r^2 \rangle$, where brackets refer to an average over all geometric configurations of the system, after N excursions or steps of length 1. Since the larva's foraging activity has a constrained or restricted heading probability in three dimensions, recourse can be made to a large body of literature dealing with such systems namely, the statistical mechanics of chain molecules and in particular their growth by sequential covalent linkage. The definitive exposition of such systems is the treatise by Flory (1969) and his development of an expression for the characteristic ratio, $C_N \equiv \frac{\langle r^2 \rangle}{N l^2}$ of a polymer chain with N angle restricted covalent bonds of length 1. Following the notation of Flory (1969), the identical development can be done making appropriate changes consistent with the different heading probability distribution being used.

The configurational average of the projection of the i + k-th excursion vector on the i-th is

$$\left\langle \tilde{l}_i \cdot \tilde{l}_{i+k} \right\rangle = l^2 \prod_{j=i}^{i+k} \cos\theta_i \quad , \tag{7}$$

where $|\tilde{l}_i| = 1$ for all i and θ_i is the angle heading regarding the i - 1-th as zero. This expression can then be used in the expression for $\langle r^2 \rangle$ which is

$$\left\langle r^2 \right\rangle = N l^2 + 2 \sum_{i<j}^{N} \left\langle \tilde{l}_i \cdot \tilde{l}_j \right\rangle \quad ,$$

where $0 < i < j \leq N$. Thus from the above

$$\begin{aligned} \langle r^2 \rangle &= N l^2 + 2 l^2 \sum_{i<j}^{N} \prod_{m=i}^{j} \cos\theta_m \\ &= N l^2 + 2 l^2 \sum_{k=1}^{N-1} (N-k) \prod_{m=i}^{j} \cos\theta_m \quad , \end{aligned} \tag{8}$$

where in the last step we have combined terms where j - i = k. In this case the last step is not totally justified because the set $\{\theta_i\}$ does not have the property that for j - i = j′ - i′ = k

$$\prod_{m=i'}^{j'} \cos\theta_m = \prod_{m=i}^{j} \cos\theta_m$$

as in the analogous development for the polymer chain where $\theta_i = \theta_j$ for i, j≤N. However, in our development the θ_i are normally distributed about the initial heading, and since the ensemble average is desired, the average over θ, $\langle C_N \rangle_\theta$, where such an identity is correct is computed and the derivation follows accordingly. To show this replacing $\prod_{m=i}^{j} \cos\theta_m$ by $\left\langle \prod_{m=i}^{j} \cos\theta_m \right\rangle_\theta$ we must show that $\left\langle \prod_{m=i}^{j} \cos\theta_m \right\rangle_\theta = \left\langle \prod_{m=i'}^{j'} \cos\theta_m \right\rangle_\theta$ when j′ - i′ = j - i = k. Because of the probability distribution of the θ_m we get,

$$\begin{aligned} \left\langle \prod_{m=i}^{j} \cos\theta_m \right\rangle_\theta &= \frac{1}{[2\pi I_0(k(c))]^N} \int_{-\pi}^{\pi} \cdots \int \left[\prod_{m=i}^{j} \cos\theta_m \right] e^{k(c)(\cos\theta_1 + \ldots \cos\theta_N)} d\theta_1 \ldots d\theta_N \\ &= \left[\frac{I_1(k(c)}{I_0(k(c)} \right]^{j-i} = \rho^{j-1}(c) \quad . \end{aligned}$$

Thus for j - i = j′ - i′ = k

$$\left\langle \prod_{m=i'}^{j'} \cos\theta_m \right\rangle_\theta = \left\langle \prod_{m=i}^{j} \cos\theta_m \right\rangle_\theta = \rho^k(c) \quad .$$

Thus

$$C_N = \frac{\langle r^2 \rangle}{Nl^2} = 1 + 2 \sum_{k=1}^{N-1} N\rho^k(c) - \frac{2}{N} \sum_{k=1}^{N-1} k\rho^k(c)$$

from the above expression for $\langle r^2 \rangle$ and using the relation for $\left\langle \prod_{m=1}^{j} \cos \theta_m \right\rangle_\theta$ just derived. Now since $\rho^k(c) \leq 1$ for all c, we have via the geometric series the relationship

$$C_N(c) = \frac{1 + \rho(c)}{1 - \rho(c)} - \frac{2}{N} \rho(c) \frac{[1 - \rho^N(c)]}{[1 - \rho(c)\ ]^2} \quad . (9)$$

Thus our estimate of the distance traveled after N excursions, R_N, by an anchovy larva of length L in a concentration of food particles c is given by

$$R_N = (Nl^2\ (L)\ C_N\ (c))^{1/2} \quad , \qquad (10)$$

where $C_N(c)$ is given above. The excursion length or step size l is shown as a function of L, an explicit relationship of which will be given later.

Model of attack rate in various concentrations of food prey

The random walk model derived above constitutes the quantitative relationship between the behavior of the larval anchovy and of food prey concentration. Since this relationship is expressed in terms of a distance which is a function of a given prey concentration, it constitutes a geometric connection between behavior and prey environment. Also, since the number of excursions and larval length are known for any distance traversed in a given prey environment, one can easily calculate the energy debt incurred by these excursions from the relationship derived by Vlymen (1974). However, an element of crucial importance to any growth simulation is an assessment or estimate of the amount of energy or food taken in by the larva in the course of these foraging excursions.

A widely held concept in fish growth simulations used in estimating energy input or ration size is that of search volume. That is, one assumes or determines experimentally a given visual perceptive area, which when multiplied by swimming speed and prey concentration during foraging gives an estimate of the amount of food consumed by the fish. Such models, however, severely underestimate the minimum environmental food content necessary to meet basic metabolic and activity caloric requirements, primarily because they assume the fish react and successfully capture every available prey organism that enters their perceptive field. Even the most cursory observation of laboratory reared anchovy larvae will reveal this to be false and demonstrates the necessity for a more sophisticated and realistic approach to the problem. Because of the absence of adequate empirical data to formulate a well grounded relationship between feeding rate and food consumption, an alternate theoretical solution to this problem will be presented and the results of the proposed theory compared with the data gathered in the laboratory.

Observations of feeding anchovy larvae reveal that feeding during foraging can be basically regarded as a two event system. The anchovy larva swims in discrete steps or units mentioned earlier and referred to as excursions. At the end of each excursion the larva either sights an appropriate prey particle and commences an attack or does not attack. During the episodes where attacks take place only one appropriate prey is perceived and attacked even though many identical acceptable prey may be in the same area. Because of the nature of the subsequent attack sequence (Hunter 1972), the anchovy larva ends up many perceptive distances away from the region where the attack was commenced and hence must initiate the whole forage procedure again – in a new area. There is also an extremely low incidence of attacks occurring immediately one after another, i.e. attacks separated by nonattack excursions. These observations lead to two important assumptions which will be used in the theoretical development to follow:
(i) Each excursion is associated with a new random sample of the environment by the larva via the perceptive volume, and
(ii) attacks on prey occurring immediately one after another, occur with a non-zero but infinitesimally small probability.
We cannot proceed, however, with only these two assumptions to a development of the attack rate of a larval anchovy in various concentrations of food prey until we make the one additional assumption that
(iii) the three dimensional distribution of prey particles is locally random.

It is important to understand that this last assumption does not mean that the prey particle distribution is random, an assumption made by most growth models. In fact, a crucial feature of this work will be the importance of exactly the opposite condition, i.e., nonrandomness, or global contagion on the growth of the anchovy larvae. Assumption (iii) implies only that within the scale of the anchovy larva the prey distribution is spatially random or manifests extremely low degrees of contagion. Large scale contagion, however, is extremely important and will be considered quantitatively later in the section on prey distributions and environmental geometries.

From assumption (i) we know that each excursion presents the anchovy larva with a new sample of the prey field, the volume of the sample being determined by the size specific reactive perceptive volume of the larva. From Hunter's (1972) measurements of the 95% confidence limits of the reactive perceptive field for anchovy larvae feeding on dense concentrations of similar sized prey organisms, we can regard the reactive perceptive volume as a segment of a specific solid of revolution. Hunter's (1972) figures 7 and 8 provide that this volume be equivalent to a circle of radius 0.37L lying in the plane of motion with one point on the circumference coincident with the larval snout and a diameter parallel to the direction of motion rotated approximately 53° about an axis passing through the snout and perpendicular to the direction of motion. This volume corresponds to a portion of a torus formed by the corresponding circle but with the distance to the rotation axis taken as one circle radius. The volume for a complete rotation is then $2\pi^2 r^3$ and for a 53° rotation the volume is

$$V_p = .294\, \pi^2 r^3 .$$

Using the numbers given above we get

$$V_p = .147\, L^3 \quad , \tag{11}$$

where L is the length of the larva.

Before using the relation above let us examine the consequences and underlying assumptions in the use of the perceptive volume concept and the possible modifications of that concept for more generality. The perceptive volume concept is an attractive and simple one but suffers from the fact that it is not prey size dependent nor is there one simple method generally agreed upon to delimit the boundary of such a volume. The limits used here are 95% confidence intervals and the geometry of the field chosen by eye fit to the data. No detailed visual field studies were done to determine 95% confidence limits in three dimensional space nor is prey size varied over a wide enough range in the data available to elucidate the functional relationship between these two variables even with a priori fixed perceptive field boundaries or geometries. However, for the purposes of this model the visual field concept gives a reasonable estimate of the perceptive field. Thus, assume that the volume calculated above is proportional to the real visual field for any size prey and, in general for any larval size, the field being larger for large prey and smaller for small prey,

$$V_{p_r} = k_v\, (d_p)\, V_p \; ,$$

where $k_v(\bar{d}_p)$ is a monotonically increasing function of mean prey diameter $\bar{d}_p$. Since data are insufficient to evaluate the function $k_v(\bar{d}_p)$ but data on smaller larvae exist to test the theory to be developed on attack rates, the k_v appropriate for this set of data can be determined and retained throughout the model. The net effect is to underestimate the visual sample size for larger larvae which feed on larger, but scarcer prey but is appropriate to first feeding larvae which feed on smaller, more abundant prey. Since the attack rate is derived from probabilities of occurrence of prey in the visual sample, this choice of k_v will not have as large an effect on the model were one to determine k_v for larger larvae.

Thus the true or corrected visual field V_{p_r} is calculated as $k_v\, V_p$ where k_v is now not a function but a constant and V_p is as given previously. The attack model can now be developed by determining the k_v that yields the best fit to the data or, alternately, corrects V_p to a functional visual field. This is different than comparing observed with expected values of attack rates obtained by an adjustable constant since the model is nonlinear and k_v occurs within the model as an independent variable and not a constant. Thus, good correlation between observed and expected values of attack rates can be regarded as support for the general model hypothesis and not an artifact of variable manipulation. The constant k_v is introduced only to obviate some of the inaccuracies and simplicities of the perceptive volume concept as they have been discussed.

From assumption (i) at each excursion the larva is confronted by a perceptive field of volume $k_v V_p$ or a visually evaluated sample of the prey field of the same volume. Then with assumption (iii) and an acceptable* volumetric prey concentration of λ the probability of k particles in the perceptive field is Poisson distributed and is given by

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* It will be shown later that as anchovy larvae grow older their food size preferences change so that even in the face of

$$P(k) = e^{-\lambda k_V V_P} \frac{(\lambda k_V V_P)^k}{k!} \quad .$$

In a prey size compensated visual field, we can assume that the minimum number of prey particles in the perceptive volume necessary for awareness by the larva is one. The probability of one or more acceptable particles in the visual field is given by

$$P(k \geq 1) = 1 - \exp(-\lambda k_V V_P) \quad .$$

This is termed the probability of 'awareness' of prey in the visual field.

Now the probability of attack on a food prey must be less than or equal to the probability of awareness because the larva makes decisions about the appropriateness of the prey of which it is aware. Although as shown, the animal is sampling visually from a concentration of λ, the probability of awareness must be multiplied by the probability of occurrence of the acceptable size range in the population as a whole to obtain the probability of attack

$$P\,(\text{Attack}) = P\,(k \geq 1)\; P\,(\text{Acceptable Size Range}).$$

The acceptable prey size range is determined as the difference between a length dependent lower bound which is known from observations of larvae collected from the ocean and an upper bound chosen as the maximum mouth diameter. Calling these two limits d_L and d_u respectively, and E_1 the event 'attack' we can rewrite the equation above as,

$$P\,(E_1) = P\,(k \geq 1)\; P\,(d_L \to d_u) \quad , \tag{12}$$

where $P(d_L \to d_u)$ represents the probability of prey sizes in the mean diameter range of d_L to d_u. If E_2 is defined as the event 'not-attack' we have together with E_1 a two-event Markov chain from which can be constructed the stochastic matrix using the above probabilities, assumption (ii), and hence allowing calculation of the mean recurrence time, μ_1, for the attack event. If the excursion frequency is given by f_E the attack rate, $\dot{A}$, can be identified simply as

$$\dot{A} = f_E\,(\mu_1)^{-1} \tag{13}$$

A two event Markov chain stochastic matrix contains four elements or transition probabilities, p_{ij}, where p_{ij} refers to the probability of the event E_j given that the event E_i has occurred at the previous trial or excursion or alternatively the probability of the transition $E_i \to E_j$. I choose to identify p_{11} as $\delta \ll 1$ according to assumption (ii) and because of the requirement that any stochastic matrix satifies the relation $\sum_k p_{jk} = 1$, p_{12} is automatically determined as $1 - \delta$; I also identify $P(E_1)$ above with p_{21} and hence p_{22} with $1 - P(E_1)$. The resulting stochastic matrix is then

$$P = \begin{pmatrix} \delta & 1-\delta \\ P\,(E_1) & 1-P(E_1) \end{pmatrix} .$$

The event E_1 is persistent and aperiodic and hence in this case

$$\underset{n\to\infty}{p_{11}^{(n)}} \to \mu_1^{-1} \quad ,$$

where $p_{11}^{(n)}$ is the probability of finding the system at time r + n in state E_1 given that at time r it was also at E_1 (Feller 1957). For this two event system it can be shown, taking $\delta \approx 0$ (Feller 1957), that the $p_{jk}^{(n)}$ matrix is given by

$$p^{(n)} = \frac{1}{P\,(E_1) + 1} \left[\begin{pmatrix} P\,(E_1) & 1 \\ P\,(E_1) & 1 \end{pmatrix} + \begin{pmatrix} (-P(E_1))^n & -(-P(E_1))^n \\ (-P(E_1))^{n+1} & (-1)^n (P(E_1))^{n+1} \end{pmatrix} \right] .$$

whence

$$\underset{n\to\infty}{p_{11}^{(n)}} = \frac{P(E_1)}{P(E_1) + 1} \text{ yielding } \mu_1 = \frac{P(E_1) + 1}{P(E_1)} \quad .$$

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abundant smaller prey a certain size range is selected. Thus λ above can be more appropriately regarded as a function of length. However, this is not accomplished in the final model by using a specific length dependent function for λ but is determined separately each time because of its multifactorial nature and reinserted iteratively into the model as needed. Thus the length dependence of λ will not be shown explicitly in the equations to follow, but will become manifest as the whole model is described.

To test this theory and also to determine k_v we have recourse to a single block of data collected, using very young larvae at a variety of temperatures and feeding on a laboratory-grown stock of the dinoflagellate *Gymnodinium splendens* (Hunter 1977). The exact size distribution of this stock is known from multichannel Coulter Counter* analysis and the variable temperatures allows for testing the theory on animals with basically the same visual apparatus but at different excursion frequencies. Before testing the theory, however, the relationship between excursion frequency and temperature must be determined.

Hunter (pers. comm.) has collected data on swimming speed for anchovy larvae of different lengths and at various temperatures from 13° to 19° C. By averaging the swimming speed in body lengths (B.L.) – sec^{-1} for each temperature, the sets of data corresponding to larval lengths of 0.6, 0.8, 1.0, and 1.2 cm yield a straight line with least squares equation (B.L.) – $sec^{-1} = 0.110T - 0.941$, where T is in degrees Celsius.

From Hunter (1972) we know that at 17° to 18° C the mean excursion frequency for feeding larvae of all sizes is 1.57 excursions-sec^{-1}. From this swimming speed data it is seen that at temperatures higher than 16° C there appears to be no further increase in swimming speed with temperature. Part of this trend is artifactual because of the random walk character of the motion. That is swimming speed is determined as distance per time but distance increases as the square root of the number of excursions which is temperature dependent. Thus, at high temperatures or excursion frequencies the slope of the swimming speed versus temperature curve should decrease as indeed it does, even though the excursion frequency per se is not exhibiting this behavior. Hence, given the inflexion point at T = 16° C of the swimming speed versus temperature curve which corresponds to an excursion frequency of 1.57 excursions-sec^{-1} the body length per second curve may be converted into an excursion frequency curve by simply multiplying by $\frac{1.57}{0.110(16)-0.941} = 1.916$ or excursion frequency $= 0.211T - 1.80$. That is, the two curves are isomorphic.

In addition to the excursion frequency relation for various temperatures, the distributional characteristics of the prey population used in Hunter (1977) are needed. It is generally agreed (Lasker 1975) that a minimum critical sized particle is necessary before even the smallest first feeding anchovy larvae will attack prey. Although no well defined lower limit to prey size exists, larvae of approximately 5.0 mm in length, as occur in the data we are considering, will require prey particles at least 40 μm in mean diameter before any significant feeding takes place. Thus, for purposes of calculation we will take

$$P(E_1) = P(k \geq 1)\, P(\bar{d}_p \geq 40\ \mu m).$$

Now the concentration of *G. splendens* in the data of Hunter (1977) is ~ 200 cells-cm^{-3} and multi-channel Coulter Counter analysis of this culture reveals that

$$P(\bar{d}_p \geq 40\ \mu m) = 0.168.$$

Thus all data are available to test the theory except for the determination of k_v. The theoretical attack rate in attacks-min^{-1} for these data is then given by

$$\dot{A} = \left[\frac{P(k \geq 1)\, P(\bar{d}_p \geq 40\ \mu m) + 1}{P(k \geq 1)\, P(d_p \geq 40\ \mu m)}\right]^{-1} [0.211T - 1.80]\ 60\ sec\text{-}min^{-1},$$

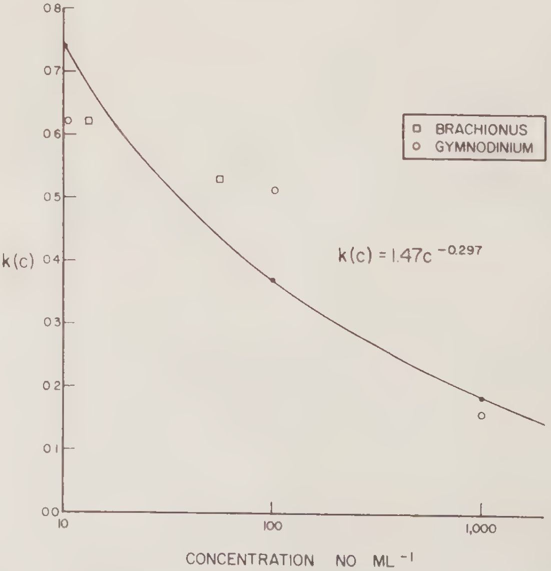

Fig. 1. The food prey concentration dependent dispersion coefficient of the circular normal distribution, k(c), computed from the heading probabilities in Hunter and Thomas (1973) for anchovy larvae feeding on the dinoflagellate *Gymnodinium* and the rotifer *Brachionus*.

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* Use of trade names does not imply endorsement by the National Marine Fisheries Service.

where $P(k \geq 1) = 1 - \exp(-29.4\, k_v L^3)$ and the values in parentheses are derived from the appropriate constants already given to these data.

Calculation of $\dot{A}$ with the previous equation for larval lengths of 0.45–0.50 cm and temperatures of 13.1° to 18.9° C as given in Hunter (1977) yields an extremely good correlation with measured attack rates as shown in Figure 2, with $k_v = 0.108$. As predicted for small sized prey $k_v \leq 1$, and although k_v as alluded to earlier is prey-size dependent, we will retain the k_v determined here for all size prey and regard the length dependent volume visual field as given by

$$V_{p_r} = 0.0159\, L^3 .$$

A brief discussion of this attack rate model is in order, together with some modifications to make it correspond specifically to the larval anchovy. As is obvious, this model is not species specific save for the inclusion of a perceptive volume indigenous to the larval anchovy. Of great interest is the observation that at any specific excursion frequency the attack rate increases asymptotically with prey concentration. This is a feature found in numerous studies on plankton grazing rates in marine animals (Steele 1974a) and is a gratifying and a priori unexpected result of the Markov model. However, because of this character the attack rate exhibits a maximum asymptotic value that obviously occurs as $P(k \geq 1)P(d_L \to d_u) \to 1$. Since $\mu_1 \to 2$ in this case the model predicts at any excursion frequency a maximum asymptotic attack rate of $\dot{A}_{max} = f_E \mu_1^{-1} = f_E/2$ or an attack sequence every other excursion. Obviously such high attack rates cannot be maintained for physiological reasons and to use this model effectively it is necessary to limit the maximum attack rates to those observed in the laboratory. Hunter (personal communication) has data which reveal a maximum attack rate of ~ 10 strikes-min^{-1} under all circumstances. If we take the mean excursion frequency to be 1.57 excursions-sec^{-1}, this requires the recurrence time for the attack event to be no less than 9.46 excursions-attack^{-1} to yield a maximum attack rate of 10 attacks-min^{-1}. Thus, the attack recurrence time will be taken as the calculated value above for $\mu_1 > 9.46$ and equal to 9.46 when the calculated μ_1 is less than 9.46.

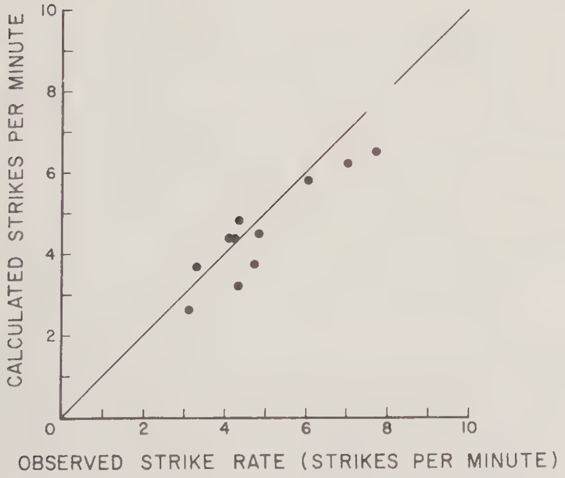

Fig. 2. Observed prey strike rate for 0.5 cm anchovy larvae feeding on laboratory grown stock of *Gymnodinium* with known size distribution from Hunter (1976a) plotted against strike rate calculated from Markov chain attack rate model (see text).

With the inclusion of this asymptotic attack recurrence time we now have an attack rate model that yields results similar to those found by experiment and is completely consistent a posteriori with the laboratory determined criteria for successful larval anchovy feeding as outlined in Lasker (1975) and the qualitative and quantitative description of anchovy larval feeding behavior as contained in Hunter (1977).

However, an adequately descriptive attack rate model cannot be used to determine energy input primarily because not all attacks on prey are successful. This characteristic of the anchovy larval feeding behavior has been well documented and quantitatively described by Hunter (1972). The relationship elucidated by Hunter suggested that success of capture of various appropriate food types displayed the form of a learning curve and the data obtained was adequately represented by the equation

$$\text{percent success} = 93.2 \log_{10} t - 33.30 ,$$

where t is the larval age in days. It should be pointed out that success in capture of prey is only important for determining energy input. Each attack has an associated energetic cost to the larva whether or not the attack is successful and constitutes one of the energy debts incurred by the organism in the course of foraging.

Thus the rate of successful attacks on prey is given by the Markov attack rate given above times the success percentage associated with the age of the larva.

Prey size distribution and environmental geometries

The attack event probabilities $P(E_1)$ given in the preceding section depend quantitatively on the characteristics of the prey size distribution. The size of the particle consumed, which will be regarded later as the mean in the acceptable range or segmental mean of the prey size distribution, is also dependent on the characteristics of the prey distribution. The only efficient means of integrating a prey size distribution into a dynamic model that has ecological significance is to use a size distribution that is representative of the acal particle spectrum in the region where anchovy larvae are found.

A particularly ubiquitous and simple size distribution found in nature and one which possibly could apply equally well to the size distribution of living organisms in the ocean is the hyperbolic size distribution. A thorough discussion of this distribution and its applicability to the description of various naturally occurring particulate systems can be found in Bader (1970). According to Bader (1970) this size distribution is characterized by an associated cumulative number distribution of the form

$$N_d = k_H d^{-m} \tag{14}$$

where N_d is the number of particles cm^{-3} greater than mean diameter d and m and k_H are characteristic constants. The term hyperbolic is given to the distribution because on linear scales the function can be plotted as a hyperbola when $m = 1$.

The inshore region of the Los Angeles Bight is one of the major spawning grounds of the northern anchovy. To get an assessment of the mean particle size distribution anchovy larvae are confronted with in this region, data from multichannel Coulter Counter analysis of Niskin casts from approximately 1 to 20 m in depth (R. Eppley pers. comm.) were averaged over the water column and plotted as a cumulative distribution via equation (14). As can be seen from Figure 3, the hyperbolic distribution adequately describes the total particulate size distribution. Least squares evaluation of the constants k_H and m in equation (14) yield the values of 446,963 and 2.81, respectively. It must be stressed, however, that various environmental and biological conditions can affect the magnitude of these constants, but the effects are remarkably small. Recalculation of the constants k_H and m during blooms of dinoflagellates for instance, does not affect m and has only a limited tendency to increase k_H. Thus we will regard the constants calculated here as representative of the particle size distribution in the major spawning ground of the northern anchovy and the distribution which will be used in modeling larval growth.

From the hyperbolic relation (14) two important quantities necessary for the model are derived, namely the segmental means $\bar{d}(d_L, d_u)$ and the range concentration $C(d_L, d_u)$.

If the number of particles-cm^{-3} with mean diameter $> d$ is $k_H d^{-m}$, then the probability of a particle having a mean diameter between d_L and d_u is given by

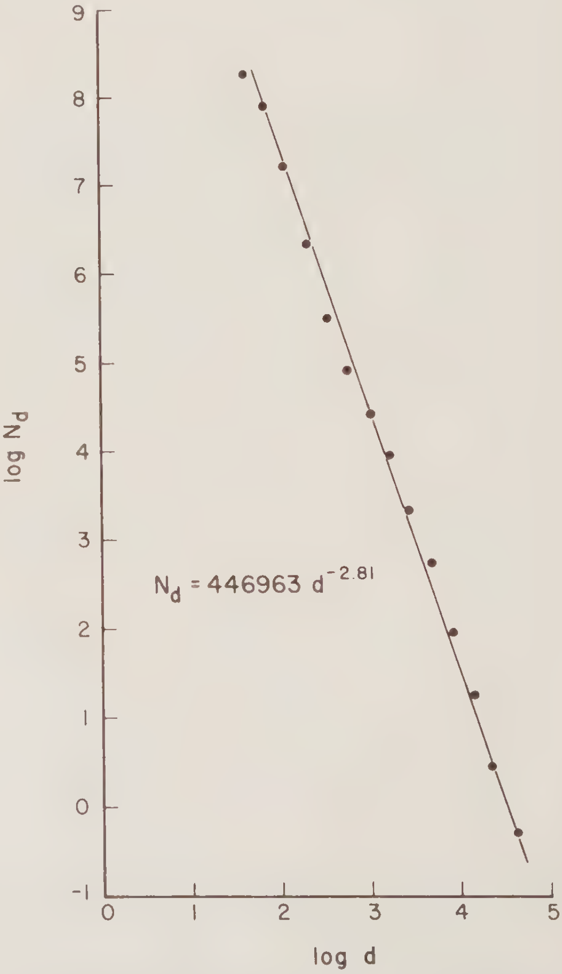

Fig. 3. Hyperbolic distribution of particle sizes in the Los Angeles Bight where N_d is the number of particles cm^{-3} greater in mean diameter than d, where d is in μm.

$$P(d_L \leq d \leq d_u) = \frac{k_H d_L^{-m} - k_H d_u^{-m}}{N_t} ,$$

where N_t is the total number of particles cm^{-3} greater than some extremely small reference size. Now for anchovy larvae only particles > 20 μm in smallest dimension are found in the gut at even the earliest stages of the larval period (Berner 1959). Thus we take $N_t = k_H(20)^{-m}$ and $P(d_L \leq d \leq d_u) = \frac{d_L^{-m} - d_u^{-m}}{(20)^{-m}}$. Since the density function f(r) for this range must satisfy

$$\int_{d_1}^{d_u} f(r)\,dr = P(d_1 \leqq d \leqq d_u) \quad ,$$

$$\int_{20}^{\infty} f(r)\,dr = 1$$

and

$$f(r) \geq 0.$$

we get $f(r) = \frac{mk_H r^{-m-1}}{N_t}$. The segmental mean is then for $m > 1$

$$\bar{d}\,(d_1, d_u) = \left[\int_{d_1}^{d_u} r f(r)\,dr \Bigg/ \int_{d_1}^{d_u} f(r)\,dr \right]$$
$$= \frac{m}{m-1} \left[\frac{d_1^{(1-m)} - d_u^{(1-m)}}{d_1^{-m} - d_u^{-m}} \right] . \quad (15)$$

The particle concentration in the range d_L to d_u is simply

$$C(d_L, d_u) = k_H(d_L^{-m} - d_u^{-m}). \quad (16)$$

In the above formulations it will be noted that particle concentration and particle mean size are only between an upper and lower limit referred to as d_u and d_L respectively, because, as discussed previously, anchovy larvae of given length demonstrate a specific particle size preference in their diets. To determine these limits the field observations on gut contents in larval anchovy by Arthur (1956) and Rojas de Mendiola (1974) may be used. Although Rojas de Mendiola was concerned with a different species, namely *Engraulis ringens*, a comparison with Arthur's (1956) data for *Engraulis mordax* reveals no fundamental differences between the two species.

Certainly an upper bound, d_u, for the size preference range is the maximum width of the mouth. This does not indicate that the animal selects food prey as large as its mouth but rather the mouth size limits the maximum prey size it can eat. Data from Hunter (1977) reveals that the maximum mouth width for anchovy larvae can be adequately described by the relation,

$$d_u(L) = 54.302 + 345\,L \quad , \quad (17)$$

where $d_u(L)$ is in μm and L is in cm.

The lower size range is determined directly from the observational data quoted above. From Rojas de Mendiola (1974) and Arthur (1956) we see that as anchovy larvae get larger, the smallest prey they are observed to take also get larger. Even in the face of abundant small prey they are observed to remain true to this preference. The data suggest that up to 2.0 cm in larval length the lower size limit of food prey taken rises linearly. Above 2.0 cm larval length, however, the lower limit remains relatively constant at least up to 3.0 cm larval length. Using a linear two point equation the lower size range is given by

$$d_L(L) = 100\,L \qquad L \leq 2.0 \text{ cm} \quad (18)$$

where $d_L(L)$ is in μm and L is in cm.

It is interesting to plot $\bar{d}(d_L, d_u)$ from equation

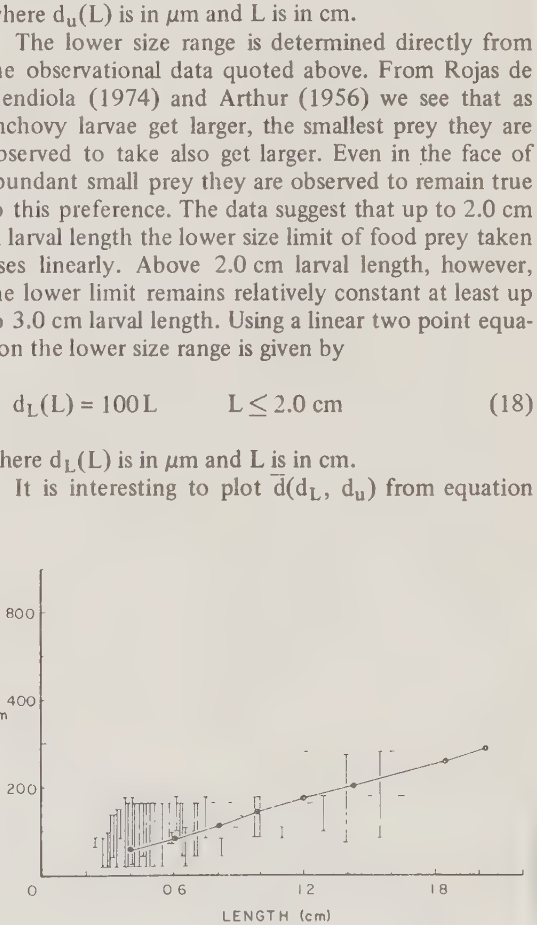

Fig. 4. Stomach content size ranges for particles found in guts of larval anchovies from Rojas de Mendiola (1974) plotted with segmental means calculated from hyperbolic particle size distribution (see text).

(15) using the $d_u(L)$ and $d_L(L)$ above and the particle distribution for the Los Angeles Bight. It is seen from Figure 4 that these means always lie within the bounds of the particle sizes actually found in anchovy larvae from Rojas de Mendiola (1974) and are almost equal to the observed means themselves. It also is observed that the mean size particle from the hyperbolic size distribution in a size range where the upper bound is increasing very rapidly is not much larger than the lower limit itself and corresponds well to what is observed in anchovy larvae feeding in a natural environment. With this quantitative concept of the particle size distribution fed on by anchovy larvae and the length dependent ranges of selection that the larvae feed upon, we can address the most complex of all environmental questions, namely prey particle microdistribution and patchiness.

Virtually no data exists on the three-dimensional distribution of prey particles of approximately 20 to 200 μm on a scale of 1 to 10 cm. It may well be asked if such a distributional scale even exists. To such questions there is no singular answer but it may be said, to quote J. H. Steele (1974b) on the structure of marine ecosystems: 'patchiness or spatial heterogeneity can occur on nearly every scale of measurement and must depend on the nature of the response of organisms to their aquatic environment.' Older descriptions of patchiness, particularly Bainbridge (1957) concentrated on discrete patches of phytoplankton a few meters wide to hundreds of square kilometers. More recently detailed distribution maps of certain species of zooplankton in a small bay (Anraku 1975) have shown the dramatic three dimensional diversity and character of plankton patchiness at scales of ~ 1 m. It, therefore, seems inevitable that when devices become available to investigate even smaller distributional scales patchiness will again be observed as a prominent feature.

Although no general model of the spatial distribution of all species in the ocean could exist, various attempts have been made to elucidate some of the relationships between the physical and biological parameters in the ocean at the mesoscale level, i.e., 10 m to 10 km, for phytoplankton. An excellent review of such studies may be found in Wroblewski et al. (1975). However, it is obvious from such studies that phytoplankton have certain advantages over zooplankton regarding modeling and that most such models elucidate only general characteristics even at the extremely large scales considered. Thus, if one is to consider the spatial characteristics of the larval anchovy food microenvironment at small scales, recourse must be made to theoretical models based on reasonable assumptions. This is exactly the theoretical analog of the situation considered experimentally in Ivlev (1961) when he analyzed the variation of food ration in fishes as a function of the aggregation of food material. The results of his study will be discussed at the conclusion of this work.

Before presenting a spatial model of the food microstructure it is important to discuss a fine point in the reasoning of the dynamics of the structure to be presented. Since the spatial characteristics of the food microstructure are a result of the operation of both deterministic and random forces, any purely deterministic model of that structure is strictly not representative. Thus the geometric properties attributed to that environment are not representative of the true environment but rather to an 'environment-like' region with well defined spatial properties. Hence, the results of interactions of a behavioral submodel with the environmental submodel really pertain only to the specific characteristics of the environmental submodel used. By the exigencies discussed above this environmental submodel may differ significantly from reality. However, the behavioral submodel, because of its secure experimental foundation, does not. Hence significant correlations observed between larval growth and environment as a result of the submodel interactions does indeed address itself meaningfully to the question of environmental effects on larval growth. Only when detailed data on the exact character of the environmental geometry is elucidated will the magnitude and significance of the correlations demonstrated in the model become known.

The theoretical determination of the spatial relationships in the environment taking into account the contagiousness of the prey population will be done using the concept of mean crowding developed by Lloyd (1967). However, even with this concept some assumptions about the nature of the underlying patchy distribution must be made. The negative binomial distribution is the one chosen here as a global description of the underlying distribution because it has been shown to be ecologically sound and fits adequately many sets of empirical data (Feller 1943, Skellman 1952). Under these conditions Lloyd (1967) demonstrated that the ratio of mean crowding, c*, to mean density c is given by

$$\frac{c^*}{c} = 1 + \frac{1}{k} \,, \tag{19}$$

where k is the nondimensional contagion parameter of the negative binomial distribution. Mean crowding as developed by Lloyd is a measure of the mean number per particle of other particles in the same patch. This, of course, implies that we have sampled the distribution with sample sizes approximately equal to the mean size of the patches which in our case is unknown. However, whatever range concentration we consider, the approximate relationship between the concentration of particles in the patch, c_p, will be regarded as related to the mean particle concentration by

$$c_p \cong c(1 + 1/k) \quad . \tag{20}$$

Given the patch concentration in the contagious distribution by equation (20) and assuming as before the particle distribution is locally random, we can calculate the distance to the nearest neighbor in the patch using Chandrasekhar's (1943) numerical solution of the Hertz distribution of the nearest neighbor in a random distribution of particles

$$R_{\text{nearest}} = 0.554 \left(\frac{g}{D}\right)^{1/3} \quad , \tag{21}$$

where g is the mean mass of a patch particle and D is the particle mass density. From the above relations this is given by

$$R_{\text{nearest}} = 0.554\,[c(1 + 1/k)]^{-1/3} \quad . \tag{22}$$

Once we have an estimate for the patch concentration we must provide some measure of the patch's geometric radius, r_{patch}. This is obviously a random variable whose value is a function of multifractional biological and physical forces. However, since we are interested in the response of a larva to a given environmental geometry we will provide a reasonable but deterministic estimate of the mean patch radius by assuming that the mean patch diameter is R_{nearest} weighted by a nondimensional factor proportional to the number of particles per patch or $c^* + 1$. That is, $r_{\text{patch}} = \frac{R_{\text{nearest}}}{2}(c_p^* + 1)$ where $c_p^* = c_p/c'$ and c' is an arbitrary reference concentration. Taking c' as $1 - \text{cm}^{-3}$ and using (22) we get the following estimate of patch radius:

$$r_{\text{patch}} = 0.277\,([c(1 + 1/k)]^{2/3} + [c(1 + 1/k)]^{-1/3}) \quad . \tag{23}$$

This will constitute our estimate of patch radius for a degree of contagion k and range concentration c.

The relation is seen in Figure 5 plotted for c values of 5, 10, and 15 particles-cm^{-3} and where r_{patch} is in cm. It can be seen that this relation has certain heuristically desirable properties. Namely, the patch radius for any degree of contagion is greater for higher mean concentrations of particles, and patch radius increases with progressively higher degrees of contagion (i.e., lower k). It is of no consequence that there exists a specific value of r_{patch} as $k \to \infty$ for any given c because in this case the behavioral model makes no distinction between patches despite a finite r_{patch} because $c_p = c$.

Thus far, only one portion of the food microstructure geometry has been determined, namely the patch radius and concentrations for any given value of k and c. To complete the structure an estimate of the mean interpatch distance and interpatch concentration is needed. This can only be done if one considers a specific volume and a specific number of particle patches. Both of these quantities are random variables if we regard one or the other as fixed. To obviate this difference and make these estimates more deterministic the same formalism is applied so that the patch itself can be regarded as the elementary particle.

Since the patches are regarded as distributed randomly in space, we use equation (2) to calculate the R_{nearest} of the patches themselves. In this case

$$g = \frac{4}{3}\pi c_p r^3_{\text{patch}} \bar{X}$$

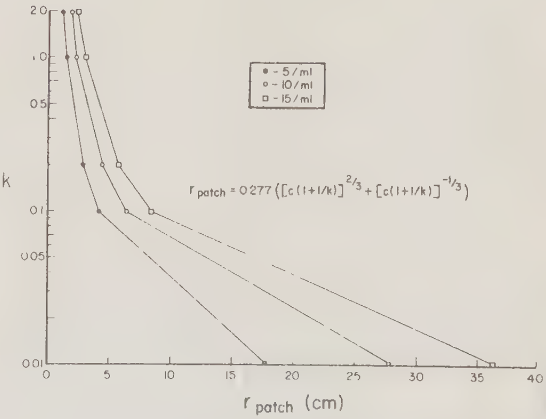

Fig. 5. Theoretical patch radius, r_{patch}, plotted as a function of prey contagion parameter, k, for three particle concentrations (see text).

where $\overline{x}$ is mean mass per patch particle. D then is the mass density not of elementary particles but of patches. Obviously an upper bound for D is patch mass per patch volume or $c_p \overline{x}$. However, this would make the environment uniformly composed of patches which is not a realistic model. Thus we will set an upper bound for D of $c \overline{x}$ rather than $c_p \overline{x}$. This yields a patchy environment that retains the important feature of patch discreteness. Thus r_{inter} in this case becomes

$$\frac{R_{nearest}}{2} = 0.277 \left[4/3 \, \pi \, (1 + 1/k) r^3_{patch} \right]^{1/3} . \quad (24)$$

The interpatch concentration will then be approximated as the value of c or the mean concentration of the system. The relationship (24) is shown in Figure 6 and demonstrates the desirable properties of increasing interpatch distance with increasing patch diameter and with degree of contagion i.e., decreasing k.

The total environmental geometry as developed here, although not derived explicitly from particle mass conservation methods, does have properties of a mass conserved system. That is, high k or low contagion yields closely spaced small patches of particle concentrations not significantly higher than the mean, whereas low k or high contagion yields widely spaced large patches of particle concentrations significantly greater than the mean. The only aberrant property of the system presented here from an ideal mass-conserved system is the assumption of the mean particle concentration for the interpatch regions. This implies that when this environmental structure is interfaced with the behavioral model larvae will grow more rapidly at high degrees of contagion than they would in an analogous mass conserved system for the same degree of contagion. However, the trends will be similar because of the basic similarities discussed.

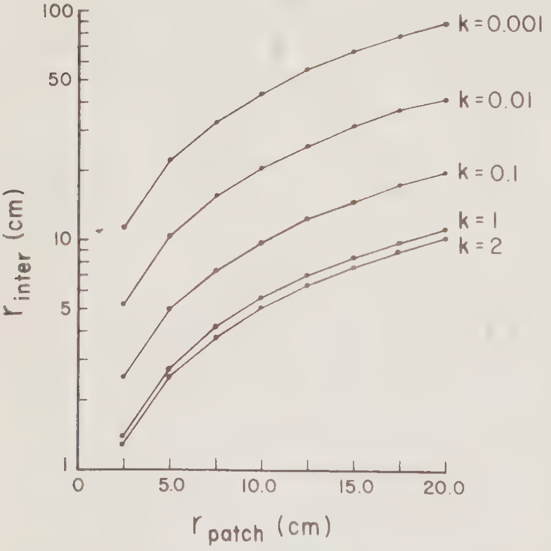

Fig. 6. Interpatch radius, r_{inter}, as a function of patch radius, r_{patch}, for five different values of prey contagion parameter k (see text).

In essence then we have an environment with explicit contagion dependent geometric and prey density parameters that can be interfaced with the behavioral submodel already developed. This interaction will yield various growth curves for larval anchovies from 0.4 to 2.0 cm in length that can be viewed as functions of these contagion dependent parameters and hence as functions of purely geometric and prey density elements and show how interactions between behavior and environmental substructure affect growth in the larval anchovy.

Additional physiological components

Certain quantitative relations for elements of the various submodels must be determined before any simulations can actually be performed. These components are not discussed in any great detail since their use has been described implicitly or explicitly in the preceding sections or will be described in the section on computer simulation.

Excursion length: The step length as a function of larval lenght l(L) in equation (10) is an example of such an element that must be determined from experimental data. Hunter (1972) provides data demonstrating that at 17° C the relationship between larval anchovy swimming speed and larval length is given by $S = 1.038L - 0.215$, where S is in cm-sec^{-1} and L is in cm. The excursion frequency at this temperature is 1.57 excursions-sec^{-1} and dividing the speed equation above by the excursion frequency yields the desired relation

$$l(L) = 0.661L - 0.136 \quad (25)$$

Maximum gut volume: A length dependent function for maximum gut volumes of anchovy larvae is also needed in the following simulation. To determine this gut content data (Hunter pers. comm.) of newly fed larval anchovies of various lengths were examined for those animals displaying the largest quantities of gut contents for any particular larval length. The food types varied from nauplii of the brine shrimp *Artemia* and the rotifer *Brachionus* for small larvae to numerous copepods of the genus *Tisbe* for larger larvae. The gut contents analysis data included the exact size and number of each prey type in the gut. The total volume of these prey in μ^3 was determined using analogies to appropriate geometric shapes. The results were analyzed by least squares and yielded the relation

$$G_{vol} = (1.30 \times 10^9) L^{1.63} \quad , \tag{26}$$

where G_{vol} is in μ^3 and L is in cm.

Caloric values of prey particles: A representative relationship between mean particle diameter and caloric value for a spectrum of food prey types acceptable to anchovy larvae is also needed for this model and was determined from data in Hunter (1977). Least squares analysis of the data yielded the relation

$$C_{particle} = (8.319 \times 10^{-11})\, d_p{}^{3.39} \quad , \tag{27}$$

where $C_{particle}$ is in calories and d_p is in μm.

Digestive times: Digestive times in anchovy larvae which will become important in our studies have not been intensively studied. Arthur (1956) provides some inferential data concerning anchovy larvae digestive times in which he concludes that digestive time depending on temperature is between 1 and 3 hours. This is a very rapid rate compared with detailed studies by Blaxter (1965) on herring larvae, a related clupeoid, in which a rate of 4 to 8 hours was observed. More recently as a result of studies in progress on predation by young adults (Hunter pers. comm.) digestion rates of 2 hours or less were observed. Thus, the digestive time of an anchovy appears to be extremely rapid and not to vary greatly throughout life as evidenced by the studies above. Also, although digestive times are temperature dependent, insufficient data on anchovy larvae are available to elucidate such a relationship. We will thus assume that the mean digestive time for a full gut by anchovy larvae of all sizes is 2 hours which is the median of the times given by Arthur (1956) and partially supported by Hunter.

Basal metabolic rate: A basal metabolic rate as determined by controlled experiments where activity has been observed to be at a minimum is not available for the anchovy larvae. However, such studies are available for sardine larvae, a similar species. Lasker & Theilacker (1962) found that the respiration rate of inactive sardine larvae was 1.33 μl O_2-mg dry wt^{-1} hr^{-1} at 14° C. From Lasker et al. (1970) we know the length weight relationship of the larval anchovy is given by

$$W = 0.3186 L^{3.3237} \quad ,$$

where W is in mg dry wt and L is in cm. Multiplying the basal respiration rate above by the length-weight relationship yields a basal metabolic rate (B.M.R.) of

$$(5.08 \times 10^{-2}) L^{3.3237} \quad . \tag{28}$$

B.M.R. in calories-day^{-1}, L in cm, and assuming a caloric equivalent of 5 Kcal-l O_2^{-1} and 24 hours-day^{-1}. This equation is very similar to the figure obtained by using Winberg's (1956) basal metabolic value for fish of 24 calories-gm wet wt^{-1}-day^{-1} which yields an alternate basal metabolic rate relation of B.M.R. = $(5.10 \times 10^{-2})L^{3.3237}$. Using equation (28) and assuming a Q_{10} of 2 we can then write the temperature and length dependent B.M.R. for larval anchovy as

$$\text{B.M.R.} = 5.08 \times 10^{-2}\, [1 + 0.1\,(T - 14)] L^{3.3237} \tag{29}$$

T in degrees Celsius.

Excursion energies: The energy required for swimming during foraging is an extremely important energetic debt and is equivalent to the energy per excursion multiplied by the excursion frequency. The energy required per excursion is given by Vlymen (1974) as

$$E_S = 27.5\, L^{4.48}$$

where E is in ergs and L in cm. According to Vlymen (1974) the efficiency of this motion is 24.6%. Converting to calories the energetic cost per excursion to the anchovy larvae is then given by

$$E_S = (2.671 \times 10^{-6}) L^{4.48} \quad . \tag{30}$$

Processing energy requirement: In all fish there is an energetic requirement for the mechanical processing of food, primarily for the manipulation of prey and intestinal propulsion of gut contents. Although this value has not been calculated for anchovy larvae it may be estimated from studies on other fish. Kerr (1971) has determined this value for trout and found that it is linearly related to the ration of the animal in the following manner

$$E_p = 0.29R \quad , \tag{31}$$

where E_p is the processing energy and R is the total energetic equivalent of the ration. This value is probably smaller than the corresponding value for a larval fish because of the different amount of musculature devoted to these processes in the larval versus the adult fish. In this study I use the above relation as an estimate of this energetic debt in the anchovy larvae.

Digestive efficiency: It is generally observed that digestive efficiency is very high in most fish species, being 80% or greater in value (Winberg 1961). However, once digestion has taken place the absorbed food has to be converted into usable energetic substrates. The efficiency of this process varies with differing food categories and with what are regarded as the conversion end-points. It is doubtful, however, that this efficiency exceeds 60% (Sharp and Francis 1976). Thus, of the daily ration, approximately 48% (i.e., 0.6 x 0.8) is available energy and is taken as the estimate of available energy for use in the model.

Conversion of excess energy growth: Assuming a caloric equivalent of 5 Kcal-g dry wt^{-1} and using the length-weight relation from Lasker et al. (1970) we have the energy difference between two lengths L_{n+1} and L_n as

$$\Delta E = 1.593 \left(L_{n+1}^{3.3237} - L_n^{3.3237}\right) \quad .$$

$$L_{n+1} = \left[\frac{\Delta E}{1.593} + L_n^{3.3237}\right]^{0.301} \quad . \tag{32}$$

Thus given an energy excess of ΔE during a day when the larval length is L_n the larval length for the next day is L_{n+1} and is given by (32).

Computerized growth simulation

The flow sheet of computer operations for the growth simulation model (Figure 7) uses the actual Algol computer names for the various functions discussed. These names, their definitions, and the corresponding equation in the text where the function and its associated discussion may be found will be used in the description to follow. The description of the simulation will follow the direction of the arrows in Figure 7 from left to right, down, and then up.

The first part of the simulation involves the establishment of initial conditions for day and length at the time of complete yolk absorption, namely $L = 0.4$ cm and $N = 0$. It is important to remember that the initial condition for the number of days does not represent time from hatching but time from complete yolk absorption. Once the initial conditions are set the iterative loop values are designated under which the simulation is to be performed. The rectangles represent these iterative loops and show that the simulation is to be performed for water temperatures of 14°, 15°, 16°, and 17° C and for each temperature the simulation executed for prey contagion or k values of 0.001, 0.005, 0.01, 0.05, 0.075, 0.085, 0.095, 0.1, and 0.15. Considering that $k = 8$ is virtually identical to a completely random distribution of prey it might appear that these k values represent unnaturally high a priori values of contagion. However, in many ocean investigations where the negative binomial has been fitted to collected data, low k values in this range have been routinely obtained (Zweifel & Smith MS*).

In the iterative loops the first two operations are the computation of the temperature dependent excursion frequency, BTFQ, and the age-dependent-success-of-capture-function, SUCL, derived in an earlier section. It is seen that the independent variable of SUCL is $N + 4$. This is so because the success of capture function was computed for days after hatching, not days post yolk absorption. A 0.4 cm larva is on the average 4 days old, hence the addition of four in the argument.

Next in order are the calculations of the length dependent upper, UPLM, and lower, LOLM, prey concentration limits as given by equations (17) and (18), respectively. These are used to calculate the interpatch concentration, CI, given by equation (16) using the hyperbolic distribution constants k_H and m determined for the Los Angeles Bight of 446,963 and 2.81 respectively. This value of CI is then used to calculate CP, the intrapatch concentration, using the loop contagion value k, which is then used to calculate the patch radius, DP, via equation (23), and the intrapatch distance, DI, via equation (24). All computed concentrations and distances are given in numbers of particles-cm^{-3} and cm, respectively.

These calculations have an important but implied geometric meaning, namely, that every ontogenic stage of the anchovy larvae, because of continuously changing food size preferences, is modulated concomitantly by continuously changing prey geo-

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* Data from a manuscript by J. Zweifel & P. E. Smith tentatively titled 'Formal confidence interval estimates for survey estimates of fish egg and larval abundance.'

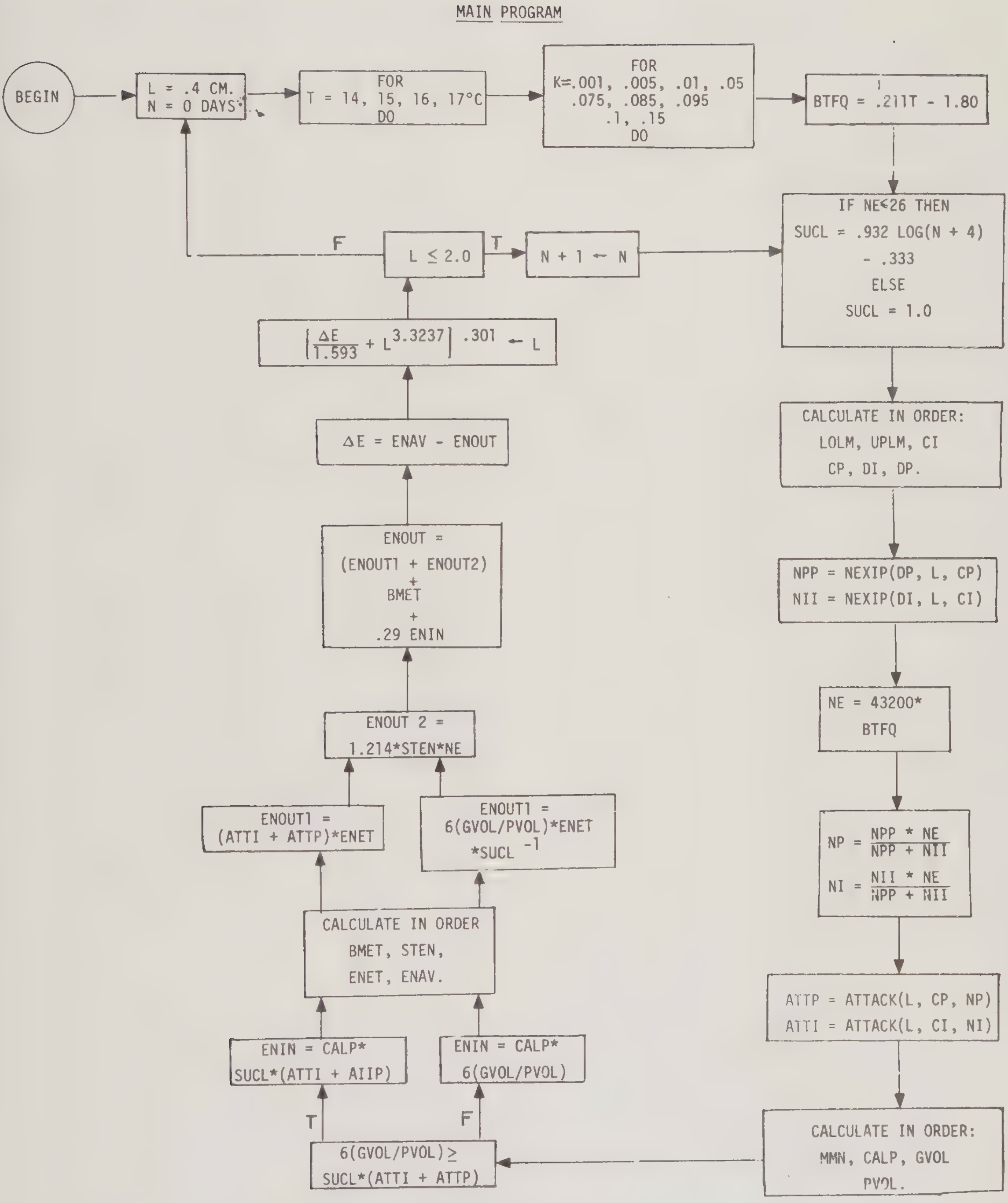
MAIN PROGRAM
BEGIN
L = .4 CM.
N = 0 DAYS
FOR
T = 14, 15, 16, 17°C
DO
FOR
K=.001, .005, .01, .05
.075, .085, .095
.1, .15
DO
BTFQ = .211T - 1.80
IF NE≤26 THEN
SUCL = .932 LOG(N + 4)
- .333
ELSE
SUCL = 1.0
CALCULATE IN ORDER:
LOLM, UPLM, CI
CP, DI, DP.
NPP = NEXIP(DP, L, CP)
NII = NEXIP(DI, L, CI)
NE = 43200*
BTFQ
NP = NPP * NE / NPP + NII
NI = NII * NE / NPP + NII
ATTP = ATTACK(L, CP, NP)
ATTI = ATTACK(L, CI, NI)
CALCULATE IN ORDER:
MMN, CALP, GVOL
PVOL.
6(GVOL/PVOL) ≥
SUCL*(ATTI + ATTP)
T
F
ENIN = CALP*
SUCL*(ATTI + AIIP)
ENIN = CALP*
6(GVOL/PVOL)
CALCULATE IN ORDER
BMET, STEN,
ENET, ENAV.
ENOUT1 =
(ATTI + ATTP)*ENET
ENOUT1 =
6(GVOL/PVOL)*ENET
*SUCL -1
ENOUT 2 =
1.214*STEN*NE
ENOUT =
(ENOUT1 + ENOUT2)
+
BMET
+
.29 ENIN
ΔE = ENAV - ENOUT
[ΔE/1.593 + L^3.3237] .301 ← L
L ≤ 2.0
T
F
N + 1 ← N

Fig. 7. Flow diagram of complete computer growth model. See text for explanation of symbols.

metries. Thus, any given value of k throughout the growth span of 0.4–2.0 cm gives rise to a continuous spectrum of spatial prey geometries.

The next sequence of calculations involves the invocation of the procedure NEXIP (D, L, C) using the parameters L and the previously calculated quantities CI, CP, DI, and DP. The procedure NEXIP (D, L, C) determines the number of steps of length given by equation (25) required to traverse a distance D in a concentration of food particles C as given by equation (10) and discussed in the first section. Thus NPP = NEXIP (DP, L, CP) is the number of excursions a larva of length L will require to traverse a patch of radius DP and concentration CP, and NII = NEXIP (DI, L, CI) is the number of excursions for a larva of the same length to traverse an interpatch distance of length DI and particle concentration CI. It will be noticed that according to equations (23) and (24) DP and DI represent respectively the mean patch radius and 1/2 the mean intrapatch distance. These numbers are used rather than the total values of patch diameter and intrapatch distance because calculations are being made of the mean growth of a larva of length L swimming through a particular prey environment for 1 day. That is, the ensemble average of such motions requires the number of larval excursions to traverse the patch radius and 1/2 the interpatch distance on the average since the patches are randomly distributed in space.

The following two calculations in the flow diagram are the number of excursions during the 12 hour foraging period, NE = 43,200*BTFQ, and the proportion of the total daily foraging excursions spent in patches, NP, and in between patches, NI. Only a 12 hour foraging period is considered because it is well established that anchovy larvae feed only during the day (Arthur 1956).

The procedure ATTACK (L, C, N) calculates the number of attacks on prey made by an anchovy larva of length L executing N excursions in prey concentration C by the method outlined in the second section. This calculation is performed differently from the example in the second section in two details. First, the recurrence time is limited by the calculated minimum of 9.46 excursions and second, we no longer multiply $P(k \geq 1)$ by $P(d_L \rightarrow d_u)$ since $P(d_L \rightarrow d_u)$ is always 1 when $P(k \geq 1)$ is calculated from the range concentration. Thus ATTP = ATTACK (L, CP, NP) is the total number of attacks on prey made by an anchovy larvae of length L in patches during the day and ATTI = ATTACK (L, CP, NP) is the number of such attacks between patches.

Next calculated is the mean size, MMN, of the particles attacked and consumed given by equation (15), CALP, the caloric value of particles of size MMN given by equation (27), GVOL, the maximum gut volume of an anchovy of length L given by equation (26), and PVOL the volume of the mean particle using standard mensuration formulae.

The calculation of the daily ration which follows is based on the following decision. If, assuming a digestion time of 2 hours, as discussed in under 'Additional physiological components', the maximum number of particles that could be processed in a day, 6(GVOL/PVOL), is greater than the number of particles successfully attacked, SUCL*(ATTI + ATTP), then the number attacked successfully is regarded as the daily ration. If the inequality is false, then although conditions may have existed for consuming more food, the most that can be processed is taken as the maximum. Thus, in the first case the daily ration in calories is ENIN = SUCL*(ATTI + ATTP)*CALP and in the second case ENIN = 6(GVOL/PVOL)*CALP.

Following this decision and selecting the appropriate value of ENIN we calculate BMET, the temperature and length dependent basal metabolic debt for 24 hours given by equation (29), STEN, the energy per excursion given by equation (30), ENAV, the available energy of 0.48 ENIN discussed above, and ENET, the attack energy of 3 STEN. This latter estimate is made from data in Vlymen (1974) and Hunter (1972).

Next, depending on the preceding decision ENOUT1, the first component of the energy debt, is calculated. This component, the energetic debt of the attacks made during the foraging period and depending on the truth or falsity of the previous decision is ENOUT1 = (ATTI + ATTP)*ENET or ENOUT1 = 6(GVOL/PVOL)*ENET*SUCL^{-1}, respectively.

ENOUT2, the second component of the energy debt is the energetic debt of swimming for a 24 hour period. If the excursion frequency remained the same during the day and night, the number of excursions made during a 24 hour period would be 2*NE. However, anchovy larvae reduce their activity at night and although we do not know the exact magnitude of this reduction, experiments with other clupeoid larvae can give an estimate of this factor. Blaxter (1973) found an activity reduction of 78.6% in herring larvae experiencing maximally decreased light levels. Thus the number of larval anchovy excursions at night using this figure would be estimated as 0.214*NE the total for day and night being ENOUT2 = 1.214*NE*STEN.

Following this calculation the total energetic debt, ENOUT, for a larvae of length L swimming for 24 hours at temperature T in a prey environment of global contagion k is estimated. This is simply ENOUT = ENOUT1 + ENOUT2 + BMET + 0.29 ENIN. The last summed debt is the cost of handling and processing the daily ration as discussed above.

The excess energy for the day, ΔE, is calculated as the difference between the available energy from the daily ration. ENAV, and the energetic debts incurred, ENOUT. This difference, if positive, is converted into a length via equation (32). If the difference is negative the process is terminated and a statement printed in the computer output that growth has ceased at day N + 1. If the new length is ≥ 2.0 cm the day is incremented by 1 and the new length used in the loop again. When the length reaches 2.0 cm the process is terminated, the loop control limits shifted and the process continued with new loop variables starting with L = 0.4 cm and N = O.

Results and discussion

The computer simulation outlined in the previous section was converted into an Algol program and executed on a Burroughs 6700 computer. Although the results of that execution can be displayed in a variety of ways because of the multifactorial nature of the problem, two methods are selected here which visually yield the greatest amount of information. In Figure 8, for each temperature selected, the average growth rate $\overline{\frac{dL}{dt}}$ in cm-day^{-1} from 0.4 to 2.0 cm is plotted against global contagion k and in Figure 9, 17° growth curves are plotted against various degrees of contagion along with a representative 17° C growth curve obtained in the laboratory. The geometric parameters of the environment that the degrees of contagion represent can be determined only by calculating the patch radius and interpatch distance appropriate for the size larva being considered because of the length dependent preference range for the particle concentration used.

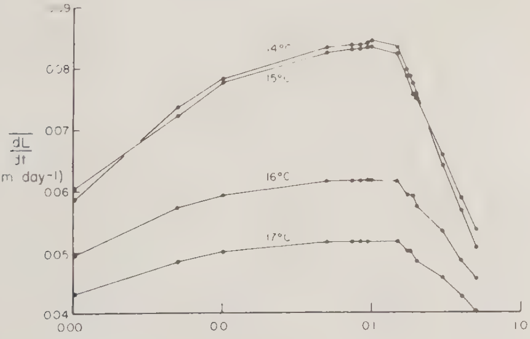

Fig. 8. Average growth rate in cm day^{-1} plotted as a function of prey contagion parameter k for temperatures of 14° to 17° C.

Neglecting the variation with temperature it can be seen from Figure 8 that the average growth rate is a nonsymmetric, nonlinear function of contagion k. For very high degrees of contagion, i.e. low k, one observes moderate growth rates that increase progressively as the degree of contagion decreases, i.e. higher k. This increase in growth rate is approximately 20% for the higher temperatures and 50% for the lower temperatures with a decrease in prey contagion of 100. A single peak maximum growth rate is obtained for all temperatures at the same degree of contagion of k = 0.10. Further decreases in contagion result in a precipitous decline in average growth rate and it may be seen from Figure 9 that the majority of this decrease is due to very slow growth in the early stages of ontogeny.

Several interesting interpretations related to fisheries can be inferred from these graphs. First, these results are in contrast to the experimental work of

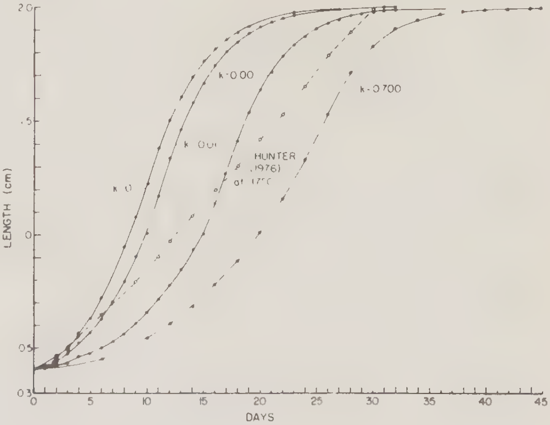

Fig. 9. Complete growth curves computed by the model for five representative levels of the prey contagion parameter, k, at 17° C along with a representative growth curve obtained in the laboratory at 17° C from Hunter (1977).

Ivlev (1961) which showed a monotonically increasing ration with increasing contagion. It seems that this is due to the different and more complete nature of the analysis done here as opposed to the two dimensional limited experimental work of Ivlev. However, although Ivlev understood the possible importance of prey geometry in fish growth studies and attempted to elucidate these relationships experimentally, he did not take into account the multifactorial nature of the problem and in particular the importance of behavior and its modification by prey contagion.

Second, one can formulate an optimal survival strategy for an anchovy larva based on these curves. It must be understood, however, that if the real ocean prey environment could be thoroughly analyzed, contagion would be anisotropic and also dependent on larval density. Thus the strategy deduced here applies strictly to the fixed geometries of the model and is simply that for long term survival prey areas yielding maximum growth rates are not advantageous because of their instability. Given that environmental forces are usually stronger in dissipating contagion at small scales than biological forces are in maintaining it, the probability is higher that contagion will decrease at any point then increase. Thus for areas yielding the maximum larval growth rate the high probability of decreases in contagion result in drastic reductions in growth rate. If we assume that total mortality of anchovy larvae for a given range of sizes from all factors is related to the time at risk in that size range, then slight reductions in contagion from the maximum growth point will greatly increase the total time at risk and hence the mortality from 0.4 to 2.0 cm. On the other hand, an optimal strategy would be to spend the majority of time in areas of higher contagion than those yielding the maximum growth rate. At these points a decrease in contagion slightly increases the growth rate while increases in contagion when they occur, slightly decrease the growth rate. Thus changes in contagion at these points do not drastically increase the total time at risk and hence the mortality from 0.4 to 2.0 cm.

This subjective explanation can be formulated in a more precise mathematical form. If the contagion varied in a simple sinusoidal manner the growth rate, as determined from Figure 8, would also vary sinusoidally.

Let the value of the contagion be that which yields the maximum growth rate, i.e., k_{max} and let the contagion vary sinusoidally over some fixed range, i.e., $k^{-\epsilon}_{max}$ to $k^{+\epsilon}_{max}$. With these conditions the growth rate would vary sinusoidally between $\left(\frac{dL}{dt}\right)_{k_{max}}$ and $\left(\frac{dL}{dt}\right)_{k^{+\epsilon}_{max}}$. The mean growth rate would then be

$$\left[\left(\frac{dL}{dt}\right)_{k_{max}} + \left(\frac{dL}{dt}\right)_{k^{+\epsilon}_{max}}\right]/2$$

and the total growth over any time period t_o would be

$$L(t_o) = \frac{t_o}{4\pi}\left[\left(\frac{dL}{dt}\right)_{k_{max}} + \left(\frac{dL}{dt}\right)_{k^{+\epsilon}_{max}}\right].$$

In a similar manner for the same degree of sinusoidal variation about $k < k_{max}$ the growth over a time period t_o would be, where $k + \epsilon \leq k_{max}$,

$$L(t_o) = \frac{t_o}{4\pi}\left[\left(\frac{dL}{dt}\right)_{k+\epsilon} + \left(\frac{dL}{dt}\right)_{k-\epsilon}\right].$$

From Figure 8 there exists an ϵ such that $k + \epsilon \leq k_{max}$, $k < k_{max}$, and

$$\left[\left(\frac{dL}{dt}\right)_{k_{max}} + \left(\frac{dL}{dt}\right)_{k^{+\epsilon}_{max}}\right]$$

$$< \left[\left(\frac{dL}{dt}\right)_{k+\epsilon} + \left(\frac{dL}{dt}\right)_{k-\epsilon}\right].$$

Thus, the length achieved after time t_o for oscillations about k_{max} is less than the length achieved for oscillations about $k \leq k_{max}$. The time at risk and hence mortality is thus greater for oscillations about k_{max} than $k < k_{max}$.

The temperature dependence of average growth rate in the model at any degree of contagion reveals a curious trend as observed in Figure 8. Except for the very high degrees of contagion one finds a reversal of the trend expected and normally observed in laboratory reared animals. That is, the lower temperatures exhibit strikingly higher average growth rates. This is most likely due to insufficient information in the model concerning substrate conversion efficiency and the fact that the total amount of food available in the model is limited, whereas in the laboratory it is not. In the model, substrate conversion efficiency is regarded as a temperature independent factor of 0.60. However, it is well known that at higher temperatures such efficiencies increase and since this factor determines the total energetically accessible ration the failure of this factor to increase appropriately with temperature and the fact that the amount of food remains fixed does not offset the increasing debts of metabolism, foraging, and feeding with higher temperature and hence one observes a lower average growth rate. Experimental information about the temperature dependence of this factor in larval fish is lacking and hence is not included. Since any model is a dynamic entity, physiological data on this relationship when available can be incorporated into the simulation.

It will also be noted in Figure 8 that the curves are not plotted beyond $k = 0.50$. Actually the curves extend beyond this point but do not extend past $k = 0.78$. That is, starting with a contagion value of $k = 0.78$, larvae of 0.4 cm after 1 day have a negative total energy balance. Thus, despite any time allowance between starvation and 'point of no return' (Lasker et al. 1970) these animals, as far as the simulation is concerned, will die. While larger animals will survive at these degrees of contagion, 0.4 cm first feeding larvae fail to survive at these lower levels of contagion.

What relationship does this value of $k = 0.78$ have to the recent studies on critical feeding in anchovy larvae? Lasker (1975) demonstrated in the laboratory that first feeding in anchovy larvae required particles $\geq 40\ \mu m$ and between 20 to 40 particles-cm^{-3}. Because the model has integrated geometric properties we can only give the range of prey concentration for interpatch and patch concentrations of particles $>40\ \mu m$ at $k = 0.78$, i.e., the contagion value just allowing for day 1 survival as determined by the computer. This particle concentration for first-feeding larvae is between 14.0 to 31.9 particles-cm^{-3}. This range of particles means that any one of the numbers could represent an environment which is structured. If only interpatch areas were sampled the value of 14.0 particles-cm^{-3} would be obtained. If, however, by some fortuitous series of events only patch regions were sampled, a value of 31.9 would be obtained. Thus, although laboratory experiments by Lasker (1975) reveal no first-feeding at average particle concentrations of 5 to 20 particles-cm^{-3} for any temperature, average concentrations without some concept of geometric structures are without meaning. This is, I believe, one of the reasons for the discrepancy between the high laboratory food requirements for minimal survival and the concentrations observed in the ocean of analogous appropriate prey types. Certainly, large concentrations of food as in *Gymnodinium* blooms are greatly advantageous but the importance of microstructure in the remainder of the environment may be of equal or greater importance.

The natural extension of such concepts is to the associated sampling problem. Fisheries scientists have never really considered the relevance of environmental microscale in larval survival but as shown above these concepts can explain a number of inconsistencies. With large scale sampling the resultant concentrations of particles determined will always trend toward the mean or the interpatch concentration. As we have seen, this concentration is almost always below that determined in the laboratory for successful first feeding. Thus, what is needed is a way of assessing the microstructure of prey aggregations on a large scale.

The actual characteristics of the larval growth curves as determined by the simulation are worthy of discussion. It can be seen from Figure 9 that they are markedly sigmoidal in character compared to the curve for laboratory grown larvae. This, I believe, is due basically to two factors. First with this model we are actually seeing the manner in which fixed geometric properties of the microenvironment modulate the larval anchovy growth. When contagion was sinusoidally varied, depending on the phase and amplitude of the oscillation, the curves, although showing the effects of the oscillations, became more linear. Also, as the environment becomes more uniform, i.e., with high k, we see that the growth curves become more parallel to the laboratory curve and essentially represent a nonstructured prey environment. Second, the foraging costs used in the model slightly underestimate these values in the early stages of ontogeny and overestimate them in the latter stages of life. This accounts partially for the rather fast growth early in ontogeny and the slower growth later on.

The inhomogeneous nature of contagion in the ocean most likely gives rise to growth curves which are very similar to those observed in the laboratory. More precisely if the value of contagion is a function of time and place, i.e. $k = k(r, t)$ and $f(k, T)$ represents the relationship between growth rate and temperature from Figure 8 then the length of the anchovy larva after time t and distance travelled r is

$$L(t, r, T) = \int_0^r \int_0^t f(k(r', t'), T)\, dr'\, dt' \ .$$

In conclusion it should be said that from this preliminary model numerous concepts emerge which justify further investigation and elaboration. The model itself as a dynamic entity is subject to further refinement and restructuring consequent to new revelations in larval anchovy physiology and behavior. However, some things seem to be clear. These are that studies of physiology and behavior are of critical importance in the understanding of any fisheries problem related to larval fish, whether it is the growth or the relationship of growth to larval mortality. Also, environmental microstructure of food particles has an intimate relationship with the behavior and physiology of larvae and this whole model can in effect be regarded as a theoretical rationalization and justification for increasing our understanding of extremely small-scale relationships in the ocean. It might be argued that this model, suffers the same defects as many biological models in that it is too deterministic. However, this determinism should properly be regarded as elucidating a species specific biological relationship which is the result of the intermodulation of several other deterministic biological parameters. As such it can be reformulated in the language of stochastic variables just as other biological systems can be reformulated today. Such a reformulation constitutes the further extension into realism which is necessary for proper understanding of the complex biological systems with which we are concerned. This work is only one step in furthering that goal of a realistic understanding of the anchovy larvae and hopefully it will serve as a starting point for other similar investigations.

Acknowledgments

I thank Reuben Lasker of the Southwest Fisheries Center, La Jolla, California, for proposing this study, donation of facilities, and constant support throughout the execution, John Hunter for numerous discussions on anchovy larvae behavior, and James Zweifel for aid in computer analysis. This work was done while I was on a NOAA Associateship at the Southwest Fisheries Center, La Jolla, California.

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DWARF HAKE OFF THE COAST OF BAJA CALIFORNIA, MEXICO

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ABSTRACT

Dwarf hake found in southern California is compared to *Merluccius productus,* the common hake found along the western coast of the United States, through morphometric measurements, meristic counts, and the electrophoresis of tissue proteins from the eye lens, vitreous humor, and muscle myogens.

Dwarf hake differs significantly from *M. productus* to suggest it may be a separate species and does not interbreed with either *M. productus* or the rarer *M. angustimanus*.

INTRODUCTION

This study was initiated to investigate the possibility of more than one stock of hake living off the coast of California and Baja California, Mexico. *Merluccius productus* is the common hake which spawns from off northern California to the tip of Baja California (Ahlstrom and Counts, 1955; Kramer and Smith, 1970). Ginsburg (1954) indicated the range of *M. angustimanus* extended northward along the west coast of Baja California to Del Mar, California, but Ahlstrom and Counts (1955) found no evidence of eggs or larvae of any species other than *M. productus.*

MacGregor (1971) collected a number of small hake off southern Baja California in January 1970, for fecundity studies. The smallest maturing male he found was 119 mm standard length (SL) and the smallest maturing female was 125 mm SL. All males 129 mm SL and longer and all females 140 mm SL and longer were sexually mature. The size at which these hake were mature was less than half that reported by Best (1963) who found only one mature fish shorter than 400 mm total length (TL). This fish was a female 380 mm TL (about 336 mm SL) with small ovaries filled with maturing eggs.

We obtained 51 frozen specimens from the same sample taken by MacGregor on January 11, 1970, at 26°07' N, 113°07' W. After thawing, all the fish in this sample had a rather red skin color. The red color is not consistent however, and has not been observed in subsequent samples. Perhaps the red color was caused by abrasion during capture as the fish had virtually no scales left because they had to be picked out of over 3,000 lbs (1,360 kg) of pelagic red crabs, *Pleuroncodes planipes,* that were caught in the same trawl. The red color faded to grey-brown when the fish were preserved in formalin.

The age of 56 hake from this and subsequent samples was determined from an examination of otoliths. The mean length at age I was similar to the mean length Best (1963) found for *M. productus,* but age groups II through V were remarkably smaller (Table 1, Figure 1). Of the 393 individual fish which we have identified and measured, the largest was only 305 mm SL and 97% of them were 250 mm SL or less.

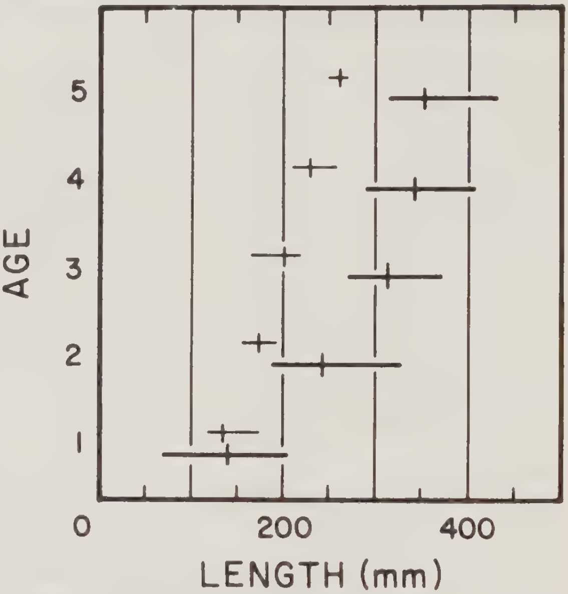

FIGURE 1. Length and age of *M. productus* (heavy bars) from Best (1963) and from dwarf hake (light bars).

From these data it appears that most of these fish are mature at age I and all are mature at age II. According to Best (1963), most *M. productus* are mature at 354 mm SL or age IV with perhaps a few of the larger age III maturing. The extremely small size at first maturity and the very slow growth rate has prompted us to refer to these small hake off southern Baja California as "dwarf hake."

TABLE 1

Mean Standard Lengths of *Merluccius productus* and Dwarf Hake by Age

AGE	Merluccius productus [*]			Dwarf hake		
	Number	Mean SL (mm)	Range SL (mm)	Number	Mean SL (mm)	Range SL (mm)
I	186	137.0	71–203	23	135.9	118–173
II	93	243.3	186–327	11	173.6	156–193
III	91	313.0	274–371	13	203.2	168–220
IV	9	342.2	292–407	7	231.0	214–260
V	10	351.9	318–433	2	261.5	253–270

[*] From Best (1963).

PROTEIN ELECTROPHORESIS

Electrophoresis of tissue proteins is an important tool for taxonomic studies. The form and structure of protein molecules are relevant sources of phylogenetic information (Sibley, 1962). Species differences in the electrophoretic patterns of muscle myogens of salmonoids were demonstrated by Tsuyuki and Roberts (1963). Tsuyuki et al. (1965) presented evidence for the virtual constancy and species specific nature of muscle myogens.

Electrophoresis of muscle myogens as well as eye lens and vitreous humor proteins was carried out in polyacrylamide gel columns according to the method described by Broome (1963). Muscle myogens of individuals of approximately 50 *M productus* tested produced patterns similar to each other but different from the patterns observed from 30 dwarf hake (Figure 2). Proteins from these and other tissues were also electrophoresed in starch gel and in polyacrylamide gel slabs, and in all cases *M. productus* differed from the dwarf hake.

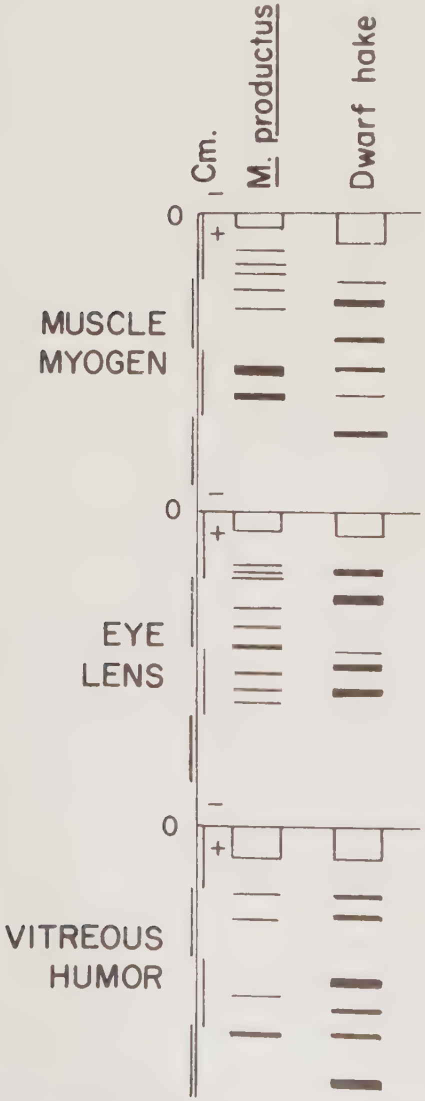

FIGURE 2. Protein patterns produced by electrophoresis in polyacrylamide-gel columns of tissues from *M. productus* and dwarf hake.

MORPHOMETRICS

We chose meristic and morphometric characters for this study according to those indicated by Ginsburg (1954) to be diagnostic for *M. productus* and *M. angustimanus.* All counts and measurements were made as he described.

Ginsburg (1954) indicated allometric growth for head length and pectoral length. Our data indicated essentially isometric growth for all the morphometric characters we examined except there did appear to be slight allometry in the snout to tip of pectoral fin for dwarf hake less than 100 mm SL (Figure 3). However, the calculated mean length of snout to tip of pectoral fin for all dwarf hake less than 100 mm SL was 52.59% SL and 52.56% SL for all those over 100 mm SL; the two are not significantly different (df = 230, F = 0.0095 ns).

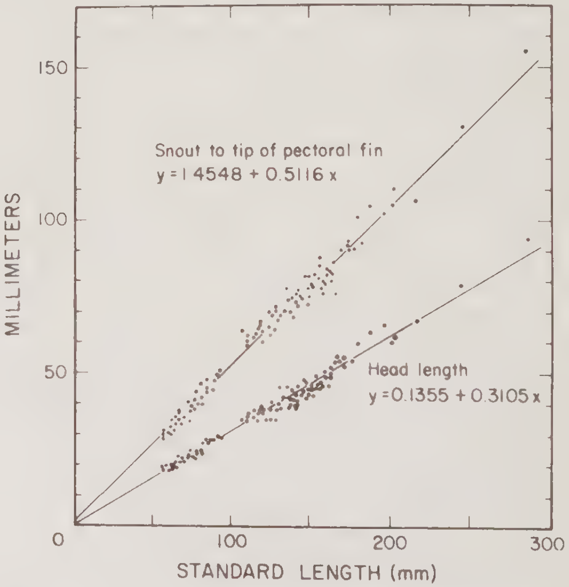

FIGURE 3. Snout to tip of pectoral fin and head length in relation to standard length for dwarf hake.

The morphometric measurements are expressed as percent of standard length (Table 2, Figure 4) and are graphically compared, as detailed by Hubbs and Hubbs (1953). The differences in the means between dwarf hake and *M. productus* are highly significant at the 0.01 level for all seven characters measured (Table 3), with dwarf hake having the largest percent of standard length for all characters.

TABLE 2

Morphometric Measurements of Dwarf Hake and *Merluccius productus* Expressed as Percent of Standard Length

Merluccius productus	N	Mean % SL	Range % SL	Standard deviation	Standard error
Snout to tip of pectoral fin	76	48.58	43.86–52.44	2.2945	0.2646
Pectoral fin length	76	19.67	11.59–23.08	2.0715	0.2376
Head length	76	28.76	25.64–33.33	1.3361	0.1498
Snout length	76	9.90	7.41–12.37	0.9761	0.1073
Maxillary length	76	13.54	10.77–17.46	1.2542	0.1438
Snout to anal fin insertion	76	45.01	37.70–50.77	1.8791	0.2243
Eye diameter	76	5.92	4.24–8.82	0.7395	0.0848
Dwarf hake					
Snout to tip of pectoral fin	231	52.57	45.78–59.26	2.3228	0.1466
Pectoral fin length	231	21.46	15.71–25.93	1.7453	0.1148
Head length	231	31.25	26.57–35.48	1.8356	0.1207
Snout length	231	10.41	8.55–13.16	0.9379	0.0617
Maxillary length	231	14.92	11.46–19.35	1.4898	0.0980
Snout to anal fin insertion	231	48.09	44.37–54.39	1.7690	0.1163
Eye diameter	231	6.58	5.33–7.94	0.5461	0.0359

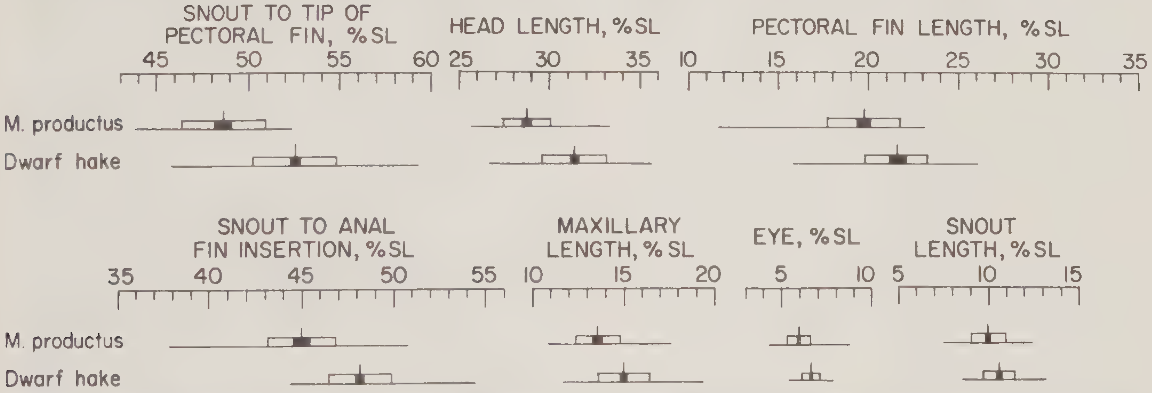

FIGURE 4. Graphic comparisons of morphometric data for *M. productus* and dwarf hake (see Table 1). The range is shown by the horizontal line and the mean by the vertical line. The solid bar represents two standard errors of the mean on either side of the mean. The open bar plus one-half of the solid bar represents one standard deviation on either side of the mean. Graphic method from Hubbs and Hubbs (1953).

Although these differences are all significant, the degree of overlap of each is so great (Figure 4) that none of the characters is very useful for field identification of individual fish; however, the combination of longer head and fin lengths and greater distance from snout to anal fin insertion gives the dwarf hake a more slender appearance than *M. productus.* In all the specimens we examined, both dwarf hake and *M. productus* had truncate or slightly emarginate caudals.

MERISTICS

In addition to the number of anal fin rays, second dorsal fin rays, and gill rakers on the first gill arch which Ginsburg (1954) indicated as the chief characters which separate *M. productus* from *M. angustimanus,* we counted vertebrae. Vertebral and fin ray counts were made from x-ray plates, gill raker counts were made directly from the fish. In nearly all cases the raker count was made from the first gill arch on the left side, in a few the left side was damaged so the right side was used. Only well formed rakers were counted, tubercles were not.

Ginsburg suggested that in some hake there might be a slight growth change in gill raker count. Since the mean standard length of our *M. productus* (218.5 mm SL) was almost twice that of dwarf hake (114.3 mm SL) we tested for growth changes. The mean number of gill rakers on the first gill arch was calculated for both species segregated into 100 mm SL size groups (Table 4). The differences in the means between size groups within either species were tested and found to be not significant at the 0.5 level.

TABLE 3

Comparison of the Means of the Morphometric Characters for Dwarf Hake and *Merluccius productus*

	M. productus % SL	Dwarf hake % SL	Difference % SL	df	F
Snout to tip of pectoral fin	48.58	52.57	3.99	306	169.03
Pectoral fin length	19.67	21.46	1.79	306	53.80
Head length	28.76	31.25	2.49	306	126.76
Snout length	9.90	10.41	0.51	306	19.63
Maxillary length	13.54	14.92	1.38	306	55.69
Snout to anal fin insertion	45.01	48.09	3.08	306	155.66
Eye diameter	5.92	6.58	0.66	306	69.33

TABLE 4

Mean Numbers of Gill Rakers on the First Gill Arch of *Merluccius productus* and Dwarf Hake Segregated into 100 mm Size Groups

	Standard length 0–99 mm		Standard length 100–199 mm		Standard length over 200 mm	
	N	Mean	N	Mean	N	Mean
M. productus	0	—	37	19.54	62	19.37
Dwarf hake	95	17.26	131	17.36	5	17.20

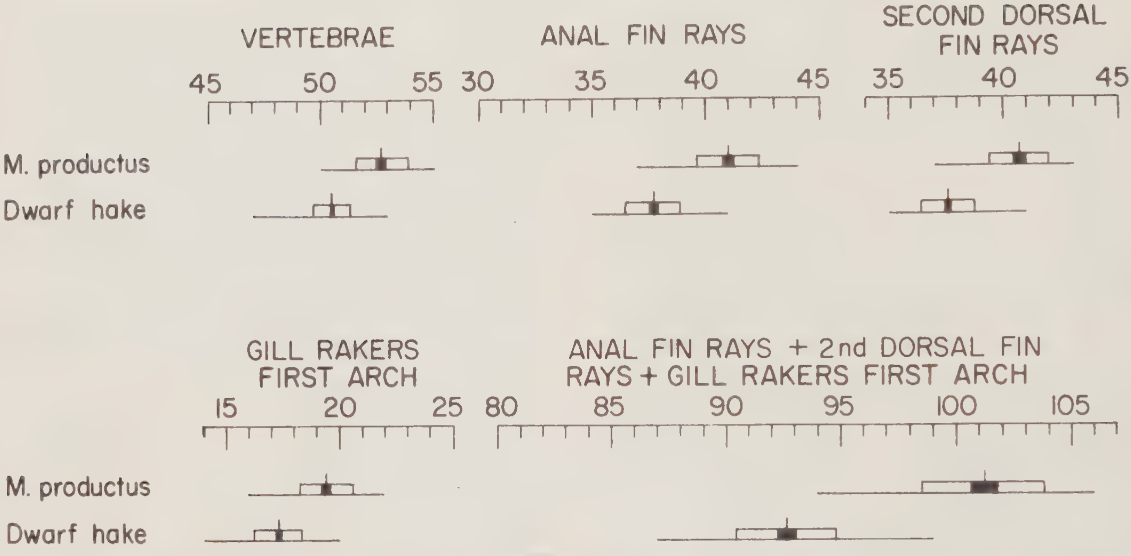

FIGURE 5. Graphic comparisons of meristic data for *M. productus* and dwarf hake (see Table 4). The range is shown by the horizontal line and the mean by the vertical line. The solid bar represents two standard errors of the mean on either side of the mean. The open bar plus one-half of the solid bar represents one standard deviation on either side of the mean. Graphic method from Hubbs and Hubbs (1953).

TABLE 5

Meristic Counts for *Merluccius productus* and Dwarf Hake

	N	Mean	Range	Standard deviation	Standard error
Merluccius productus					
Number of vertebrae	94	52.73	50–55	1.1563	0.1193
Anal fin rays	91	41.02	37–44	1.3497	0.1415
Second dorsal fin rays	93	40.69	37–43	1.3265	0.1376
Gill rakers upper limb	105	4.30	3–5	0.5904	0.0576
Gill rakers lower limb	105	15.10	13–18	0.9085	0.0887
Total gill rakers first arch	105	19.41	16–22	1.1985	0.1170
Anal + 2nd dorsal + total rakers	91	101.20	94–106	2.6759	0.2805
Dwarf hake					
Number of vertebrae	210	50.52	47–53	0.7959	0.0549
Anal fin rays	192	37.71	35–41	1.1794	0.0851
Second dorsal fin rays	175	37.58	35–41	1.2004	0.0907
Gill rakers upper limb	231	3.90	3–5	0.4913	0.0323
Gill rakers lower limb	231	13.43	11–16	0.8145	0.0536
Total gill rakers first arch	231	17.32	14–20	1.0767	0.0708
Anal + 2nd dorsal + total rakers	171	92.67	87–99	2.2566	0.1726

Dwarf hake have fewer vertebrae, anal fin rays, second dorsal fin rays, and gill rakers than *M. productus* (Table 5, Figure 5). The differences in the means for all of these characters are highly significant at the 0.01 level (Table 6). There is considerable overlap in the counts so no single character is very useful for field identification of individual fish; however, the sum of three meristic characters which are readily counted in the field, anal rays, second dorsal rays, and gill rakers on the

TABLE 6

Comparison of the Means of the Meristic Characters for *Merluccius productus* and Dwarf Hake

	M. productus	Dwarf red hake	Difference	df	F
Number of vertebrae	52.73	50.52	2.21	302	373.07
Anal fin rays	41.02	37.71	3.31	281	441.84
Second dorsal fin rays	40.69	37.58	3.11	266	381.08
Gill rakers upper limb	4.30	3.90	0.40	334	41.50
Gill rakers lower limb	15.10	13.43	1.67	334	287.23
Total gill rakers first arch	19.41	17.32	2.09	334	246.81
Anal + 2nd dorsal + total rakers	101.20	92.67	8.53	260	727.82

TABLE 7

Meristic Data From Samples Arranged From North to South

Sample number *	Latitude	Vertebrae		Anal rays		Second dorsal rays		Gill rakers		Anal + second dorsal + rakers	
		N	Mean	N	Mean	N	Mean	N	Mean	N	Mean
1	38–34°N	25	53.04	23	41.35	25	41.24	25	19.64	23	102.04
2	33–30°N	25	53.08	23	41.17	25	40.92	25	19.80	23	102.00
3	29°N	25	52.52	23	40.78	25	40.20	25	19.60	23	100.96
4	27°N	25	50.76	23	38.22	25	37.52	25	17.24	23	92.43
5	26°N	25	50.72	23	37.00	25	37.24	25	17.64	23	91.83
6	25°N	25	50.56	23	37.74	25	37.80	25	17.12	23	92.65

* Samples 1, 2, and 3 are *Merluccius productus;* samples 4, 5, and 6 are dwarf hake.

first arch, is a good tool. If we had arbitrarily separated all the hake in our samples into two groups with this combination character, those with a sum of 96 or less as dwarf hake and those with 97 or more as *M. productus,* we would have misclassified only 6 *M. productus* out of 91 and only 8 dwarf hake out of 171, for a total identification error of 5.34%.

Frederick H. Berry,[1] a National Marine Fisheries Service (NMFS) Fishery Biologist formerly at this laboratory, proposed in an unpublished manuscript that all the eastern Pacific hake from Alaska to southern Chile were represented by two species. He concluded that *M. polylepis* from southern Chile was a valid species and the other four forms, *M. productus, M. angustimanus, M. gayi gayi,* and *M. gayi peruanus,* were a single species, *M. gayi.* He postulated that the meristic and morphometric characters which had been used to separate the last four merely reflected environmentally induced differences which varied clinally over the geographic range.

Our data did not indicate such a cline; instead, we found a distinct break in both morphometric and meristic characters in the area off Punta Eugenio, Baja California, or about 28° N. We can demonstrate this by using the method described by Rothschild (1963) for graphic comparisons of meristic data.

The procedure requires samples of equal size for comparison of any single character; therefore, after we arranged our samples in geographic order from north to south, we selected randomly from the larger number of fish to produce sample sizes equal to the smallest. We counted the mean number of vertebrae, anal fin rays, second dorsal fin rays, gill rakers on the first gill arch, and the combination of anal rays plus second dorsal rays plus gill rakers for each sample arranged from north to south (Table 7).

An analysis of variance was performed for each of these characters and in all cases F was found to be highly significant at the 0.01 level (Table 8).

TABLE 8

Analysis of Variance for Meristic Data From Samples *

	df among samples	df within samples	F
Number of vertebrae	5	144	48.60
Anal fin rays	5	132	65.95
Second dorsal fin rays	5	144	63.67
Total gill rakers first gill arch	5	144	35.15
Anal + 2nd dorsal + total rakers	5	132	145.81

* See Table 7.

The ranges, means, and one ω interval on each side of the means were plotted (Figure 6). ω is a single valued parameter for judging the significance of multiple comparisons of the observed differences using Tukey's procedure (Steele and Torrie, 1960) for $\alpha = 0.01$. A mean beyond one ω interval on either side of the mean of another sample is significantly different from that sample at the 1% level. For all 5 meristic characters tested, there is a sharp break between samples 3 and 4 or at about 28° N, which does not fit Berry's clinal theory.

The morphometric and meristic data, the size at first maturity, and the differences in tissue proteins

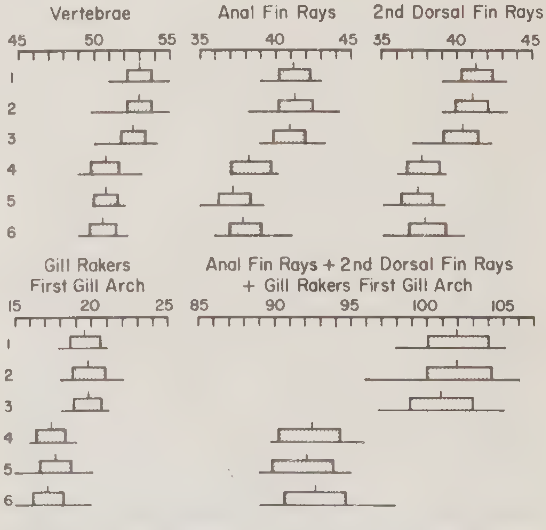

FIGURE 6. Graphic comparisons of meristic data of samples arranged from north to south. Samples 1, 2, and 3 are *M. productus,* samples 4, 5, and 6 are dwarf hake. The horizontal line represents the range, the vertical line the mean, and the solid bar represents one on either side of the mean. Graphic method from Rothschild (1963).

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[1] Berry, Frederick H. (MS) Taxonomy of the eastern Pacific hake *Merluccius.*

are convincing evidence that the dwarf hake is a species distinct from *M. productus.* However, we are not convinced that the dwarf hake is *M. angustimanus.* We have examined the specimens from off Del Mar, California, and Santo Domingo, Baja California, that Ginsburg (1954) used in his description of *M. angustimanus* and find that they fit our description of dwarf hake. Dwarf hake do not quite fit the original description of *M. angustimanus* by Garman (1899). He found 110 lateral line scales, and although we find it very difficult to get an accurate count on our specimens, the range is much higher, 125 to 150, with an average around 135. Garman's illustration and description indicates extremely long pectoral fins reaching to the fifth anal ray or beyond. Dwarf hake have relatively long pectorals but they seldom reach to the fifth anal ray and frequently do not even reach to the anal fin insertion. Garman did not count vertebrae, but C. Mathews[2] (MS) found from 45 to 49 vertebrae with a mean of only 47.02 for *M. angustimanus* from the Gulf of California; dwarf hake have from 47 to 53 vertebrae with a mean of 50.52. Out of the 83 *M. angustimanus* Mathews examined, only 2 had more than 48 vertebrae, and out of 210 dwarf hake, we found only 3 with less than 49. To adequately compare dwarf hake and *M. angustimanus* we would need to obtain fresh *M. angustimanus* from Panama suitable for electrophoresis; a series of specimens from which to take counts and measurements, and we would also need to examine Garman's type specimen, which is beyond the original scope of this paper.

CONCLUSIONS

1. There are two stocks of hake off the coast of Baja California, Mexico; *M. productus* to the north and dwarf hake to the south. The primary division between the two stocks is in the area of Sebastian Viscaino Bay or about 28° N, with some overlap in the range of the two. One dwarf hake was taken off Del Mar, California, 33° N, and one sample of 4 *M. productus* was taken off San Hipolito Bay, 27° N

2. Dwarf hake and *M. productus* are approximately the same size at age I but subsequent growth of dwarf hake is much slower than in *M. productus.* The maximum observed size of dwarf hake is 305 mm SL. The maximum reported size of *M. productus* (Best, 1963) is 800 mm TL (707 mm SL).

3. Most dwarf hake are mature at age I, and all are mature at age II. Most *M. productus* mature at age IV with perhaps a few of the larger age III mature.

4. Dwarf hake are distinctly different from *M. productus* in electrophoretic patterns produced from proteins of the eye lens, vitreous humor, and muscle.

5. Morphometrically, dwarf hake differ from *M. productus* by having longer heads, longer pectoral fins, larger eyes, longer snouts, greater distance from snout to tip of pectoral fin, and greater distance from snout to anal fin insertion.

6. Meristically, dwarf hake have fewer vertebrae, anal fin rays, second dorsal fin rays, and gill rakers than *M. productus.*

ACKNOWLEDGMENTS

We thank Pat Arasmith for her technical assistance, and Geoffrey Moser, both from the National Marine Fisheries Service, La Jolla, California, for his review and valuable comments and to Richard Rosenblatt, Scripps Institution of Oceanography, for permitting us to examine hake specimens from the Scripps collection.

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Catch Statistics and Abundance of Nehu, *Stolephorus purpureus*, in Kaneohe Bay

JERRY A. WETHERALL[1]

ABSTRACT

Catch and nominal effort statistics from the Kaneohe Bay day-baiting fishery for nehu, *Stolephorus purpureus*, were used to explore hypotheses concerning two sources of variation in baiting success: 1) nehu stock abundance, and 2) abiotic environmental variables. Baiting success was found to be positively correlated with streamflow in a major tributary to Kaneohe Bay, but was unrelated to nominal baiting effort. However, the assumptions underpinning the analyses cannot be accepted with confidence, because the available nominal effort data do not provide a good measure of effective baiting effort. A definitive understanding of nehu stock dynamics will require changes in data collection practices of the Hawaii Division of Fish and Game. In particular, detailed information on catch per set of the bait seine and on size composition of the nehu stock and catch are needed.

INTRODUCTION

The high cost of acquiring bait from the natural stocks of nehu, *Stolephorus purpureus*, has been a major obstacle to the full development of Hawaii's fishery for skipjack tuna, *Katsuwonus pelamis*. Accordingly, it has stimulated government research programs spanning a quarter of a century, seeking to develop cheaper and more reliable substitutes.

Successful creation of alternative bait supplies requires a two-pronged research effort: 1) technical development of new bait sources at unit costs permitting substitution, and 2) practical demonstration of the effectiveness of new baits and building of confidence in their use among skipjack tuna fishermen. Current status reports on research related to several alternative bait substitution schemes are presented elsewhere in this publication. Until effective substitutes are developed, skipjack tuna fishermen will continue to favor the traditional baiting practices and abundance of nehu will be of central concern to the fishing industry.

One concern is apt to be that baiting success or nehu abundance is affected by fishing pressure. The question of overfishing of Oahu nehu stocks was posed early by Hiatt and Tester (1950),[2] but the data available to them did not permit a conclusive study. Even now, details of nehu population dynamics are largely unknown, and the customary approach to nehu stock assessment has been to study an index of abundance, such as catch per unit of fishing effort. This was done by Bachman (1963), who examined the relationship between average catch per day of baiting and the number of days of baiting for several nehu fisheries, using data covering the period from 1948 through 1960. He found no evidence that fishing had diminished the stocks.

In this paper I will summarize the results of some analyses similar to Bachman's which I conducted recently. I will first show that the available unit of nominal fishing effort is probably not a good measure of effective effort, i.e., not proportional to the fishing mortality it generates. In particular, fluctuations in effective fishing effort over a wide range are severely dampened in construction of the catch per nominal effort statistics.

With the shortcomings of the available data clearly in mind, I will explore two analyses using catch statistics from the day fishery of Kaneohe Bay, one of the key baiting grounds of the Hawaii skipjack tuna fleet. The first analysis assumes that the catch of nehu per day of baiting effort is proportional to nehu abundance, and the second assumes that abundance of nehu is relatively constant and that variations in the catch per day reflect changes in catchability or availability of nehu. Results of both analyses should be viewed circumspectly.

CONSTRUCTING AN INDEX OF ABUNDANCE

For the Kaneohe Bay baiting operations, records of nehu catch (in buckets) for each trip to the baiting grounds are available. During a baiting session a boat may make as many as 10 sets of its seine before sufficient nehu are captured to support a trip for skipjack tuna. When nehu are abundant one set may be enough.

If we assume that availability of nehu and effectiveness of the fishing operation (catchability) are constant, a good measure of abundance might be the average catch per set. Unfortunately the number of sets is not recorded. The best one can do is to calculate a provisional index of abundance as the average catch of nehu per "day" of fishing, i.e., per trip to the baiting grounds.

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[1] Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, HI 96812.

[2] Hiatt, R., and A. Tester. 1950. The supply of nehu. Univ. Hawaii, Mar. Lab. News Circ. 6, 3 p. [Processed.]

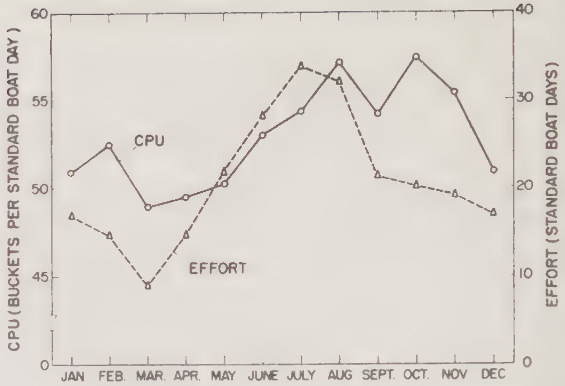

Figure 1.—Monthly average of CPU and effort, computed over 7-yr period (1966-72), for Kaneohe Bay nehu.

Separate records are available for each boat in the fleet. Four vessels, about one-third of the fleet, had fairly continuous records from 1966 to 1972. Data for the analyses were taken from these four boats. One of the vessels was selected as a standard boat, and the fishing power of each vessel relative to the standard was estimated. The average standardized catch of nehu per day of baiting (CPU) was then computed on a monthly basis, giving an 84-mo sequence.

The Hawaii Division of Fish and Game records for Kaneohe Bay also give the catch of nehu taken in the night-light operations and by users other than skipjack tuna fishermen. Thus, estimates of the total monthly nehu harvest for the Bay are available. These figures were divided by the standard index of nehu abundance to give estimates of total fishing effort, measured in standard boat days (Tables 1, 2; Fig. 1).

A major difficulty in using CPU as a measure of abundance is that skipjack tuna boats generally stay on the baiting grounds until a certain quantity of nehu is captured. This amount is determined largely by the capacity of the vessel's baitwells. A demonstration of this is given in Figure 2, for the four selected vessels, where relative fishing power or catch per day is plotted against average baitwell capacity. This shows clearly that the average catch per day is not a particularly good index of abundance, even if the number of sets per day does not vary.

During periods when nehu are abundant, the boats will easily fill their baitwells in a trip to the Bay, and the index of abundance will be truncated. Figure 3 shows the relationship between the index of abundance and abun-

Table 1.—Average catch rate of Kaneohe Bay nehu, in buckets per standard boat day, 1966-72.

	Year							
Month	1966	1967	1968	1969	1970	1971	1972	Mean
Jan.	48.57	57.60	56.37	39.96	56.42	50.10	47.39	50.92
Feb.	50.73	65.67	53.94	42.78	47.96	53.27	52.61	52.42
Mar.	55.23	49.97	37.53	51.16	46.66	51.16	50.65	48.91
Apr.	50.82	43.41	54.16	44.91	52.10	53.03	48.01	49.49
May	52.55	45.18	55.65	58.02	47.57	42.88	50.03	50.27
June	48.55	54.90	56.84	51.45	51.64	49.48	58.34	53.03
July	52.88	58.64	56.56	65.11	59.91	34.78	52.57	54.35
Aug.	57.48	57.65	53.81	58.66	61.23	50.95	59.83	57.09
Sept.	56.55	62.14	35.27	62.83	54.79	51.79	55.84	54.17
Oct.	59.03	60.41	49.84	64.42	54.18	55.92	58.04	57.40
Nov.	57.75	59.16	57.20	58.09	47.72	49.38	58.64	55.42
Dec.	62.33	50.75	33.05	57.75	47.42	50.00	55.25	50.94
Mean	54.37	55.46	50.02	54.60	52.30	49.40	53.93	52.87

Table 2.—Average baiting effort in standard boat days, Kaneohe Bay, 1966-72.

	Year							
Month	1966	1967	1968	1969	1970	1971	1972	Mean
Jan.	9.88	12.08	29.23	24.88	9.59	22.93	9.83	16.92
Feb.	12.77	6.59	17.02	6.68	22.89	23.28	11.20	14.35
Mar.	15.15	11.23	11.94	2.15	14.36	0.59	7.26	8.95
Apr.	16.23	10.94	13.44	7.99	18.77	14.29	18.64	14.33
May	24.05	14.59	22.14	15.03	16.38	37.78	22.90	21.84
June	21.01	22.35	28.74	26.70	32.69	39.59	25.50	28.08
July	36.63	26.75	37.99	22.27	37.19	52.72	23.93	33.92
Aug.	21.68	27.79	45.88	27.29	36.81	25.04	39.88	32.05
Sept.	12.25	14.63	18.32	19.38	36.45	14.67	32.86	21.22
Oct.	19.91	9.73	19.28	24.28	30.34	9.67	27.62	20.12
Nov.	19.72	21.37	26.94	19.73	29.52	2.37	14.70	19.19
Dec.	15.58	26.56	24.05	15.31	17.29	1.68	18.52	17.00
Mean	18.74	17.05	24.58	17.64	25.19	20.38	21.07	20.66

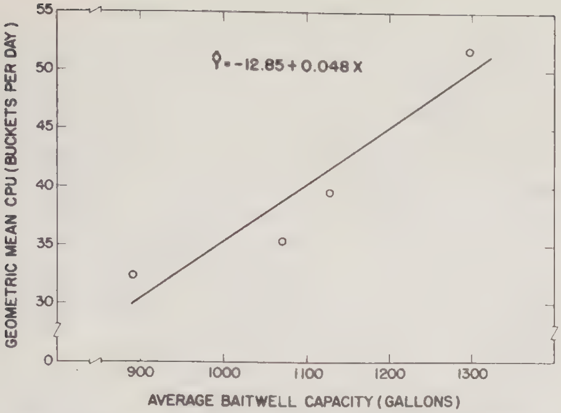

Figure 2.—Relationship between average nehu CPU and baitwell capacity for selected skipjack tuna vessels, Kaneohe Bay.

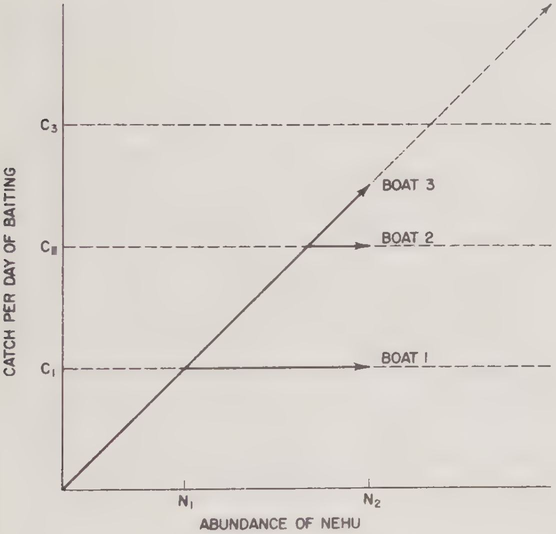

Figure 3.—Catch per day of baiting as a function of nehu abundance for hypothetical vessels with different baitwell capacities (C_1, C_2, C_3).

dance, where there are three vessels with varying baitwell capacities. In this hypothetical situation the catch per day of all three boats is a good measure of abundance as long as abundance does not exceed N_1. If the abundance increases to N_2, only the boat with the largest baitwell capacity, C_3, will still provide a comparable measure of abundance. All this assumes that the number of sets per day is constant. This is patently unrealistic as long as abundance varies.

Thus it is clear that the average catch per day has at least two serious weaknesses when used as an index of abundance: 1) the number of sets per day varies, there tending to be more sets made when nehu are relatively scarce, and 2) baitwell capacity obviously determines an upper limit to catch per day, and, since the objective is to get a full load of bait if possible, baitwell capacity tends to establish a lower bound to catch per day as well The net result is that the CPU will "underestimate" abundance when nehu are plentiful and "overestimate" it when the fish are scarce.

SOME ANALYSES

It should be recognized at the outset that any analysis of nehu abundance using the CPU rests on a set of assumptions almost certainly violated. In the following exploratory treatments of the data, I put on the blinders and assume that changes in CPU reflect similar changes in abundance of nehu with reasonable fidelity. Catchability and availability are assumed to be constant.

The empirical relationship between CPU and standardized effort was used to indicate the response of the nehu resource to fishing pressure. Since the average age of nehu in the exploited stock is believed to be only a few months, the data were first averaged by quarters of the year, producing a series of 28 points assumed to represent equilibrium conditions. If the assumptions are correct, the relationship (Fig. 4) clearly indicates no significant effect of fishing effort on average nehu abundance, over the effort levels observed. This result, not surprisingly, is the same as Bachman's.

In the analysis just discussed the only factor explicitly set out as a determinant of stock abundance was fishing effort. Effort was regarded as the input to a "black box" production process with CPU (abundance) as output. An alternative approach is to do a regression analysis in which the other factors of production, such as natural mortality and recruitment are also modeled explicitly. We may begin as before by assuming that

$$U_t = q D_t$$

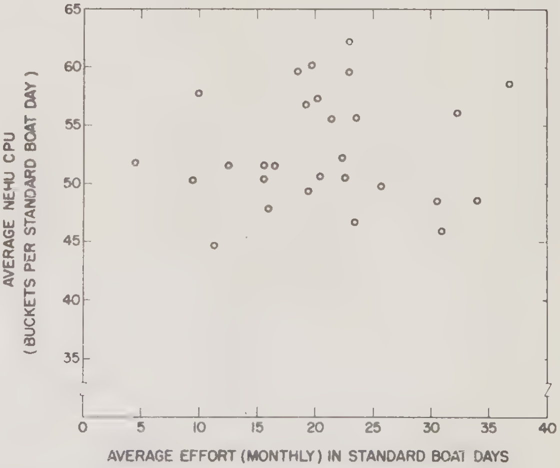

Figure 4.—Relation between quarterly average nehu CPU and standardized effort for the Kaneohe Bay bait fishery, 1966-72.

where U_i = CPU during period (month) i
D_i = average abundance of exploited stock during period i (number of nehu)
q = constant catchability coefficient.

As a first approximation,

$$\begin{aligned} U_i &= U_{i-1} \exp\left\{-\left(M + \frac{f_{i-1} + f_i}{2} q\right)\right\} + q R_i \\ &= U_{i-1} S \exp\left\{-q\left(\frac{f_{i-1} + f_i}{2}\right)\right\} + q R_i \end{aligned}$$

where M = instantaneous natural mortality rate (monthly)
S = monthly survival rate in absence of fishing mortality
f_i = standard units of fishing effort during period i
R_i = average number of newly recruited fish in exploited stock during period i.

The recruitment process may be modeled by a simple Ricker-type function, e.g.,

$$R_i = a D_{i-\delta} \exp\left\{-b D_{i-\delta}\right\}$$

where for nehu we set δ equal to 2 mo. This may be linearized by expanding the exponential in a Taylor series to obtain

$$R_i = a D_{i-2} - \frac{ab}{2} D^2_{i-2} + \ldots.$$

Alternatively, R_i may be represented by a more general polynomial in D_{i-2} without a constant term.

$$R_i = \gamma_1 D_{i-2} + \gamma_2 D^2_{i-2} + \gamma_3 D^3_{i-2} + \ldots$$

Further, since fishing mortality is assumed to be insignificant, we let

$$\exp\left\{-q\left(\frac{f_{i-1} + f_i}{2}\right)\right\} \approx 1 - q\left(\frac{f_{i-1} + f_i}{2}\right).$$

Finally, combining these assumptions we have a linear regression model, in the usual notation,

$$Y_i = \beta_1 X_{1i} + \beta_2 X_{2i} + \beta_3 X_{3i} + \ldots$$

$$\begin{array}{llll} \text{where } Y_i = U_i & & \beta_1 = S \\ X_{1i} = U_{i-1} & & \beta_2 = -qS \\ X_{2i} = U_{i-1}\left(\frac{f_{i-1} + f_i}{2}\right) & & \beta_3 = \gamma_1 \\ X_{3i} = U_{i-2} & & \beta_4 = \gamma_2 \\ X_{4i} = U^2_{i-2} & & \vdots \\ \vdots & & \end{array}$$

This regression model is a nonequilibrium form and was fitted to the monthly CPU data with $i = 3, 4, \ldots, 84$. In the recruitment component terms through the fourth degree were allowed. The concoction was fitted using a stepwise regression program. The first term accepted by the stepwise procedure was the natural mortality term. This gave $\hat{S} = 0.34$ or $\hat{M} = 1.07$ on a monthly basis. The second term accepted was the first degree recruitment term, with positive sign. Next was the second degree recruitment term with negative sign. Finally came the third degree term with positive sign. As expected, the fishing mortality term was insignificant. So was the fourth degree recruitment term.

The regression model accounted for only 20% of the variation in CPU. Still, the estimates of the coefficients have the proper signs and the estimate of M is consistent with our best guess of the life-span of nehu, judged tentatively to be about 6 mo. Bayliff (1967) studied the relationship between maximum age (Tmax) and instantaneous total mortality rate (Z) for six species of engraulids. On an annual basis his result was $Z = 6.384/T$max. Using this relation for nehu we set Tmax $= 0.5$ and obtain $\hat{Z} = 12.768$. Assuming that fishing mortality is negligible ($M \approx Z$) *we have* $M = 1.06$ on a monthly basis, compared with $M = 1.07$ from the regression analysis. The astounding correspondence between these estimates must be judged with due regard for the battery of assumptions made in each case. At best we might infer that the CPU data trace the general trend of nehu abundance, but even this conclusion is tenuous.

The preceding analysis was based on the assumption that CPU is proportional to nehu abundance, with catchability and availability constant. An alternative point of departure is to regard abundance as being relatively constant and to assume that variations in CPU are due to fluctuations in catchability or availability. A simple statement of these conditions is

$$U_i = q\, DA_i$$

where the new symbols are

A_i = overall availability during the ith time period
$= \prod_j A_{ij}$
A = availability due to factor j during period i $(0 \leq A_{ij} \leq 1)$.

Assuming a single availability process is causing variation in CPU, we factor this out (say the kth one) and take logs to obtain

$$\ln U_i = \theta + \ln A_{ik}$$

where $\theta = \ln(q D \prod_{j \neq k} A_{ij}) =$ constant.

In the bait fishery of Kaneohe Bay one factor suspected of influencing catchability or availability (it makes no difference in the analysis which process is involved) is turbidity of the water near the mouths of streams where nehu congregate. Fishermen often do not attempt to catch nehu during periods of heavy rainfall, when turbidity increases due to the boost in runoff.

An index of runoff into Kaneohe Bay is the average discharge of a major tributary such as Kamooalii Stream, which flows (via Kaneohe Stream) into the southern sector of the Bay near the city of Kaneohe. Appropriate discharge data, in cubic feet per second, are available in reports of the U.S. Geological Survey (1966-72).

Denoting the availability factor by A_i, we may write

$$A_i = \exp\left\{-\beta[d_i - d_0]\right\}$$

where d_i = Kamooalii Stream discharge in period i (cfs)

d_0 = minimum discharge level such that as $d_i \rightarrow d_0, A_i \rightarrow 1$.

Combining this with the previous equation we obtain

$$\ln U_i = \theta' - \beta d_i$$

where $\theta' = \theta + \beta d_0$.

This linear regression model was fitted to log CPU and monthly average discharge data for each year, 1966 through 1972. Logs to base 10 were used. Only two of the regressions were significant, at the 1% level. The other five were not significant. However, six of the seven correlation coefficients were negative, as expected, with values ranging from -0.16 to -0.86. The model was also fitted to all 84 data points, yielding a highly significant regression and a correlation of -0.36.

Finally, the availability model was fitted to the log of the geometric mean of CPU, and the average discharge, with the means computed over the 7 yr (Fig. 5). The regression is highly significant with a correlation coefficient of -0.71. If the assumptions of this analysis are correct, we may take this as evidence that availability, catchability or both are reduced during periods of high rainfall (January through April) and enhanced when streamflows drop (June through October).

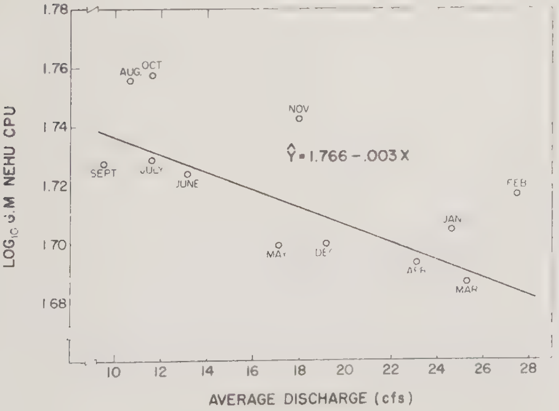

Figure 5.—Regression of log CPU on the average discharge of Kamooalii Stream at Kaneohe. Monthly data averaged over 1966-72.

THE NEED FOR BETTER DATA

The last analysis above suggests that variations in catch per unit of baiting effort may be due largely to changes in availability or catchability arising from exogenous abiotic variables such as runoff, turbidity, etc. If this is so, we can have little confidence that catch and effort statistics, taken alone, will provide useful measures of nehu abundance, particularly when short-term changes are of interest. This applies equally to measures based on catch per set and those based on catch per day. Still, the results of the exploratory analyses presented here are based on assumptions not easily accepted. While the first analysis indicated no long-term effect of baiting effort on nehu abundance, it is quite possible that there are important short-term effects of baiting effort which are erased from the CPU index in the smoothing processes discussed earlier.

A more definitive analysis of nehu stock dynamics and the relative importance of baiting effort and environmental variables in the regulation of baiting success requires a much stronger data base than is now available. At the minimum, reporting requirements for statistics on nominal baiting effort should be extended to include information on the number of sets made each day by each vessel. In addition, catches of nehu should be sampled systematically and frequently to determine size and age composition, so that more detailed modeling can be done. The responsibility for data collection in the nehu fisheries rests jointly with the Hawaii Division of Fish and Game and with members of the aku fishing industry.

ACKNOWLEDGMENTS

A draft of this paper was reviewed critically by Gary T. Sakagawa. Thomas S. Hida and Richard N. Uchida contributed materially through helpful discussions.

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Evaluation of Bait Substitution Schemes in Hawaiian Fishery for Skipjack Tuna, *Katsuwonus pelamis*

JERRY A. WETHERALL[1]

ABSTRACT

A systematic procedure is presented for judging the feasibility of bait substitution schemes in the Hawaiian fishery for skipjack tuna, *Katsuwonus pelamis*. Over the period 1968-73, the opportunity cost of nehu, *Stolephorus purpureus*, the bait now in use, peaked twice a year: during the first half of July when skipjack tuna catch rates were high and during the second half of December when the ex-vessel price of skipjack tuna was high. The opportunity cost averaged $4.78/lb, and increased by over 100% during the period, due mostly to a rise in ex-vessel price of skipjack tuna.

Feasibility of a bait substitution scheme during any season requires that unit production costs are less than opportunity costs of acquiring nehu and that the quantity of bait produced does not exceed the amount usable. Judgment of feasibility rests on some critical assumptions concerning such factors as the amount of nehu per bucket in the bait fishery, and the attractiveness of substitute baits relative to nehu. These must be substantiated through field experiments and sample surveys.

INTRODUCTION

For many years the Hawaiian fishery for skipjack tuna, or aku, *Katsuwonus pelamis*, has suffered a persistent case of stagnation. In spite of a rising consumer demand for tuna products and an ample exploitable resource, the average annual aku harvest has not been increased. Further, only one new vessel has entered the aku fleet in the last two decades, while many deteriorating boats have been retired and not replaced. The roots of this malaise were recognized long ago—a short supply of an essential ingredient, live bait, and failure of the fishing industry and supporting government agencies to develop substitute or alternative bait supplies in a rather high-risk investment environment.

The baitfish problem is a classic economic problem of technological substitution and its key elements may be conveniently summarized as in Figure 1. This shows the joint behavior of the two key variables, unit production costs and usage rate, for two hypothetical alternative baits and for nehu, *Stolephorus purpureus*, the principal bait now in use. In this two-dimensional phase space, the industry is now at "A," and moving upwards on the nehu curve with rising costs and essentially constant usage rate. The conversion path, illustrated by a dotted line, shows how an expanding aku industry would presumably switch from nehu to a first substitute bait, then to a second alternative bait as economic considerations dictated. Discontinuities in the conversion path represent points of substitution. Ideally we would be able to forecast such a path for a variety of alternative baits, or at least to determine the points of intersection which indicate conditions favorable to the introduction of substitutes. The illustration used here assumes that the two hypothetical substitutes are not yet feasible. In fact, the present positions of the cost paths for alternative baits, relative to the nehu curve, are uncertain. Research in progress may show, for example, that the "Alt 1" substitution scheme could now satisfy the present usage rate (about 170,000 lb/yr) at a unit cost less than the present opportunity cost of nehu (the opportunity cost for nehu used in fishing averaged $4.78/lb over 1968-73)

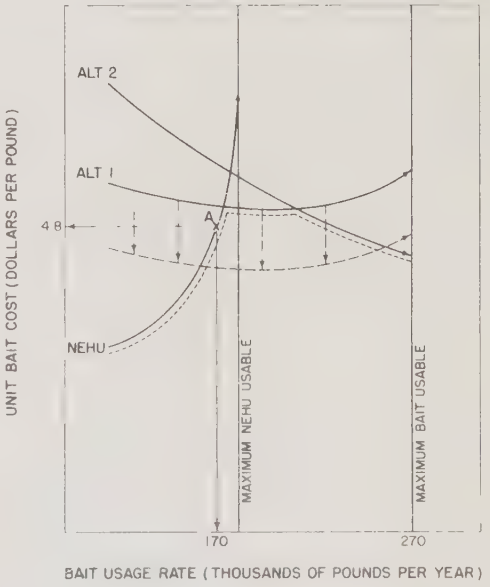

Figure 1.—Hypothetical relationships between unit bait cost and usage rate for nehu and two alternative baits. Dotted line is conversion path. Dashed line indicates uncertainty in position of "Alt. 1." In recent years the industry has been approximately at point "A."

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Solution of the baitfish problem clearly depends on success in two area: 1) technical development of alternative bait supplies at unit costs permitting substitution and 2) practical demonstration of the effectiveness of new baits and the building of confidence in their use among aku fishermen. Several determined efforts have been made along both lines, without much success (e.g., Shomura 1964; Shang and Iversen 1971). At present, two technical alternatives are under consideration, one involving the transportation of northern anchovy, *Engraulis mordax*, from California to Hawaii in special tankers aboard roll-on/roll-off freighters and the other involving local mass-culture of the topminnow, *Poecilia vittata*. The anchovy transport alternative has been field tested rather extensively by the National Marine Fisheries Service, Honolulu Laboratory, for the past year, and topminnow culture, considered a possibility in Hawaii, is being pursued experimentally by the Hawaii Institute of Marine Biology of the University of Hawaii (Herrick 1977).

Before the feasibility of either of these schemes can be properly evaluated, the basic substitution curve for nehu must be elucidated. The purpose of this paper is to set out simple, systematic procedures for determining the present position of the nehu curve and for judging the feasibility of alternative bait substitution schemes.

THE OPPORTUNITY COST OF NEHU

The principal difficulty in constructing a substitution curve for nehu is that there is no free market mechanism to measure the unit cost of nehu, i.e., the value of nehu to fishermen. Instead, the worth of nehu must be appraised in terms of the value of opportunities foregone in the capture of the bait. The opportunity cost of a unit of nehu is simply the value of the aku catch which could be obtained if a unit of baiting time was spent in aku fishing, adjusted for the difference in operating costs. It is the price the fishermen could pay for nehu, in lieu of gathering bait themselves, with no difference in their potential profits.

If we let P_1 denote the fleet's profit under the present system of baiting, and let P_2 represent profit under a new system in which some fraction of bait needs is fulfilled by a substitute, we may state the basic relations as

$$P_1 = \pi \cdot CR \cdot B - k_1 DF - k_2 DB - \overline{K}$$

and

$$P_2 = \pi \cdot CR \cdot B \left(\frac{DF + DB}{DF}\right) - k_1 \;(DF + \lambda DB) - k_2(1 - \lambda)\, DB - \overline{K} - k_3\, \lambda B \left\{\left(\frac{DF + DB}{DF}\right)\right\}$$

where π = ex-vessel prices of aku (\$/lb),
CR = catch rate; pounds of aku landed per pound of nehu used (lb/lb),
DF = number of days of fishing (old system),
DB = number of days of baiting (old system),
B = amount of nehu used in DF days of fishing (old system) (lb),
λ = proportion of baiting time in old system converted to fishing time in new system,
$\overline{K}$ = fixed costs, or costs independent of the number of days fished, the number of days baited or the amount of bait used (\$),
k_1 = operating costs for a day's fishing (\$/day),
k_2 = operating costs for a day's baiting (\$/day),
k_3 = price of bait purchased under new system (\$/lb used).

The problem now is to find the value of k_3 which satisfies $P_1 = P_2$. This value is the opportunity cost, OC, and is easily found to be

$$OC = \left(\frac{DB}{DF + DB}\right) \left\{\pi \cdot CR - \frac{DF}{B}\,(k_1 - k_2)\right\} .$$

This is, in substance, equivalent to the result of Shang and Iversen (1971), but is put in a different form and is derived in a more direct and less convoluted manner. Note that the solution for OC is independent of the conversion rate, λ.

For most practical purposes the difference in operating costs may be neglected, and the opportunity cost may be approximated by

$$OC = \left(\frac{DB}{DF + DB}\right) \;\pi \cdot CR . \qquad (\$/\text{lb})$$

Thus the opportunity cost of nehu may be considered as the product of three factors: 1) The proportion of potential fishing days now spent baiting, 2) the ex-vessel price of aku, and 3) the amount of aku landed per unit of nehu used.

TEMPORAL VARIATION IN THE OPPORTUNITY COST

Feasibility of any alternative to nehu will, of course, require that costs of that bait, per unit used in fishing, be no greater than the opportunity cost of nehu. Of particular significance will be any temporal variation in the value of nehu. A substitution scheme may be quite promising during seasons or years of high aku catch rates, say, but be altogether infeasible otherwise.

To establish the seasonality of the opportunity cost, data from the aku fishery and the baiting operations were analyzed. The data represented a 6-yr period, 1968-73, and were obtained directly from the catch records submitted by aku fishermen to the Hawaii Division of Fish and Game. The computations were based on statistics concerning all baitfishes taken in the daytime for aku fishing. Thus the label "nehu" on the results which follow is meant to indicate only that nehu is the predominant species involved, accounting for over 90% of the total bait catch.

Annual Variation

The range of annual variation in the opportunity cost of nehu and the three component factors is shown in Figure 2. From 1968 through 1973 the opportunity cost more than doubled. Over the same period there was a general increase in the proportion of days baited and in the average catch of aku per pound of nehu used. But the dominant force in increasing the opportunity cost has been a sharp rise in the average aku price. This increased by 80% over the 6-yr period.

The statistics plotted in Figure 2 are also given in Table 1 which presents, in addition, the monthly means of the opportunity cost for each year.

Seasonal Variations

Seasonal patterns of variation in the opportunity cost and its components were determined by computing 6-yr weighted averages of the appropriate biweekly statis-

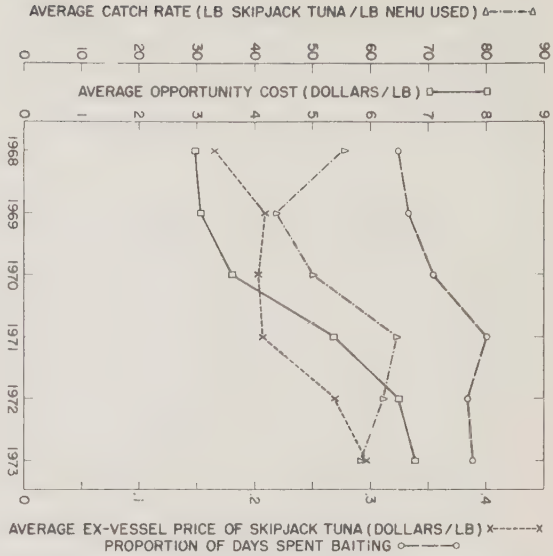


Figure 2.—Trends in the average annual opportunity cost of nehu and in its major components over 1968-73.

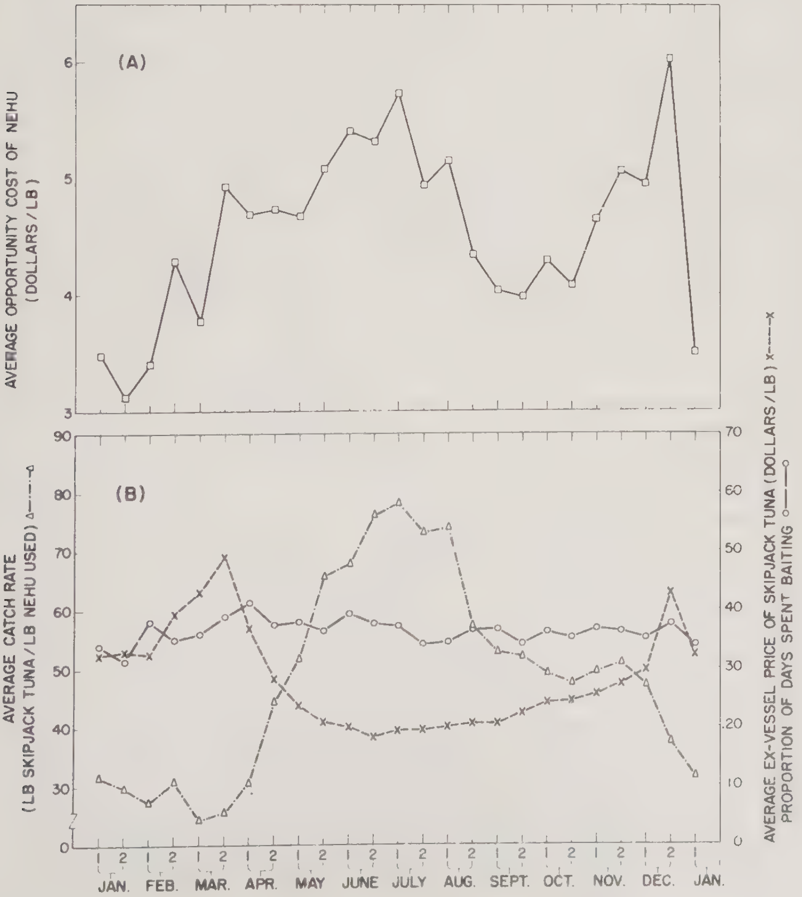


Figure 3.—Seasonal variation in (A) opportunity cost of nehu, and (B) its major components, based on biweekly statistics averaged over 1968-73.

tics. The results are shown in Figure 3 and Table 2. The top panel (A) of Figure 3 shows the seasonal pattern of the average opportunity cost of nehu. The *OC* rises from a low in the last half of January to a peak in the first half of July, drops sharply to another low in September and turns upward again to reach its highest value of the year in late December. There is a twofold variation in the average biweekly *OC* during a year.

In the bottom panel (B) of Figure 3, the seasonal behaviors of the three component factors are displayed.

Table 1.—Variation in average opportunity cost of nehu (by month), proportion of days baited, aku caught per nehu used, ex-vessel aku price, aku caught per trip, and annual aku catch for 6-yr period, 1968-73.

	1968	1969	1970	1971	1972	1973
Average opportunity cost ($/lb)						
January	2.25	4.39	1.60	3.27	4.46	3.43
February	2.22	3.48	4.63	2.58	4.83	7.05
March	2.80	3.30	2.22	4.50	7.43	6.18
April	2.83	3.58	2.49	4.59	8.60	7.78
May	2.84	2.84	2.85	6.17	7.85	7.58
June	3.01	3.50	2.74	7.40	6.87	7.93
July	2.66	3.05	4.24	6.08	7.23	8.34
August	3.32	2.50	3.43	4.67	7.85	6.86
September	2.85	2.61	4.80	4.51	4.97	3.35
October	3.34	2.56	4.01	5.02	4.37	4.96
November	3.16	2.58	4.79	7.00	5.41	6.60
December	5.10	2.89	3.78	6.72	7.31	7.37
Annual mean	2.98	3.05	3.61	5.38	6.51	6.80
Proportion of days baited	0.325	0.334	0.355	0.402	0.386	0.390
Aku caught per nehu used (lb/lb)	55.5	43.8	50.0	64.8	62.5	58.6
Ex-vessel aku price ($/lb)	0.165	0.209	0.203	0.207	0.270	0.297
Aku caught per trip (lb/trip)	4,163	3,327	3,836	6,475	5,763	5,588
Annual aku catch (metric tons)	4,218	2,692	3,332	6,004	4,948	4,859

Table 2.—Seasonal variation in proportion of days baited, aku caught per nehu used, average ex-vessel aku price, average opportunity cost of nehu, average aku catch, present bait usage rate and potential bait usage rate. Estimates are weighted means of biweekly statistics covering a 6-yr period, 1968-73.

Month	Biweekly period	Proportion of days baited	Aku caught per nehu used (lb/lb)	Average ex-vessel price of aku ($/lb)	Average opportunity cost of nehu ($/lb)	Average aku catch (10^2 lb/2 wk)	Present bait usage rate (lb/2 wk)	Potential bait usage rate (lb/2 wk)
January	1	0.340	31.6	0.325	3.49	1,126	3,562	5,397
	2	0.315	29.8	0.330	3.11	1,019	3,420	4,993
February	1	0.381	27.2	0.328	3.41	1,238	4,550	7,350
	2	0.351	30.8	0.397	4.30	756	2,455	3,782
March	1	0.361	24.3	0.432	3.78	642	2,640	4,132
	2	0.391	25.7	0.492	4.95	883	3,436	5,642
April	1	0.415	30.5	0.371	4.70	1,597	5,235	8,949
	2	0.378	44.2	0.284	4.74	2,651	5,997	9,642
May	1	0.380	51.9	0.238	4.69	4,520	8,709	14,046
	2	0.367	66.0	0.210	5.09	6,608	10,012	15,817
June	1	0.395	68.1	0.201	5.41	8,000	11,748	19,418
	2	0.378	76.4	0.184	5.32	9,995	13,083	21,033
July	1	0.375	78.5	0.195	5.74	9,931	12,651	20,241
	2	0.342	73.6	0.197	4.96	9,487	12,890	19,589
August	1	0.347	74.3	0.200	5.16	8,994	12,105	18,537
	2	0.367	57.5	0.207	4.36	6,090	10,592	16,733
September	1	0.367	52.9	0.208	4.04	4,177	7,895	12,472
	2	0.342	52.2	0.223	3.98	3,620	6,935	10,539
October	1	0.363	49.2	0.242	4.31	3,439	6,990	10,973
	2	0.352	47.4	0.245	4.09	3,435	7,247	11,183
November	1	0.369	49.6	0.255	4.66	2,767	5,579	8,842
	2	0.365	51.0	0.272	5.06	2,274	4,459	7,022
December	1	0.352	47.2	0.298	4.94	2,162	4,580	7,068
	2	0.377	37.3	0.430	6.04	1,268	3,399	5,455

The proportion of days baited does not vary over a wide range—from about 32% to 42%. It is not an important determinant of seasonal variation. Perhaps the most significant factor in fluctuations of the *OC* is seasonal change in the catch rate. From a low point in March this component more than trebles in the next 4 mo. The catch rate then begins a steady downturn which continues over an 8-mo period, except for a slight rise in November.

The third component of the *OC*, the ex-vessel price of aku, is very responsive to seasonal changes in the supply of aku on local markets and is thus inversely related to the catch rate (Fig. 3B, 4). The price considered here is the weighted average of the individual prices for fresh fish and for aku delivered to the Hawaiian Tuna Packers cannery. Though in recent years there has been a negotiated minimum price for aku sold on the fresh fish market, it is effective only during the summer season of high aku supply, when most of the aku landed are absorbed by the cannery. In months of short supply, when a relatively large share of the aku catch is sold fresh, the fresh fish price is well above the minimum level.

As shown in Figure 3B, the highest average prices occur in March, and these correspond to the annual minimum in catch rate. As the supply of aku is increased by the steady rise in catch rates during April, May, and June the aku price drops to a June low. During the second half of the "average" year the reverse pattern is observed. There is one brief deviation in the pattern; during the late December holiday season the high demand for aku bids up the price sharply, but by mid-January this effect disappears.

THE FEASIBILITY LINE

In the search for substitute baits, important decisions will have to be made concerning the scale of operations of transport or culture schemes and the extent of bait needs which the substitution schemes are intended to fulfill. A small pilot project might be viable only if its operation was restricted to the relatively brief period of highest opportunity cost for nehu. In most schemes it is likely that as the scale of operations is increased the unit costs of bait production or delivery will be reduced, though at a diminishing rate, and a greater share of total bait needs can be satisfied.

There are two obvious conditions which must be met to establish the feasibility of an alternative bait program: 1) During the period of each year when the substitution scheme is operating, the opportunity cost of nehu must not be less than the unit costs of the alternative bait (appropriately adjusted for mortality between delivery and usage), and 2) the quantity of bait produced by the scheme must not exceed the potential amount usable during the period. Figure 5 shows how a particular substitution scheme, producing bait at \$4.50/lb used, generates a feasible period of about 7 mo—5 mo in the spring and summer and 2 mo at the end of the year. During this period, according to Table 2, about 190,000 lb of bait could be used. For each point on the ordinate there is a different maximum usage rate. Together these form the feasibility line or demand curve shown in Figure 6. Substitution schemes producing more bait than can be used or producing bait at a cost exceeding the critical cost will fall in the infeasible region to the right of the line. As the opportunity cost of nehu increases, the curve will of course shift upwards.

EVALUATING ALTERNATIVE BAIT SYSTEMS

The feasible region of Figure 6 defines the set of substitution schemes which may be considered as alternatives to the current practice of using nehu only. Each (hypothetical) scheme in the region will produce an increase in profits to the aku fleet. In addition, there presumably will be benefits to the processing sector of

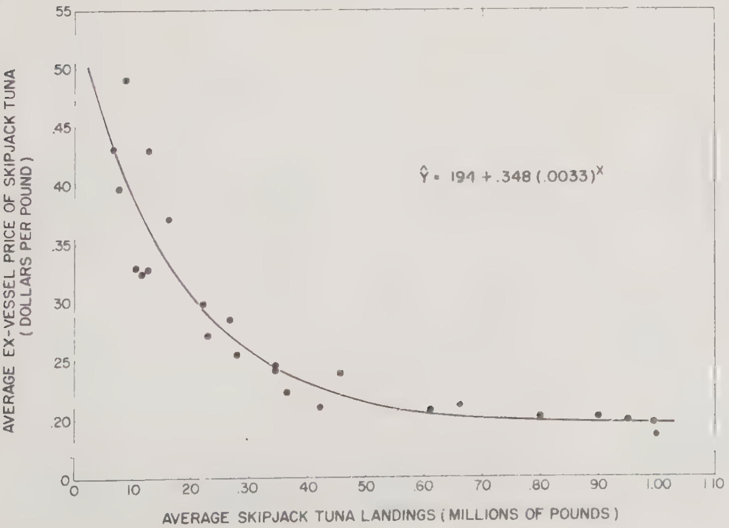
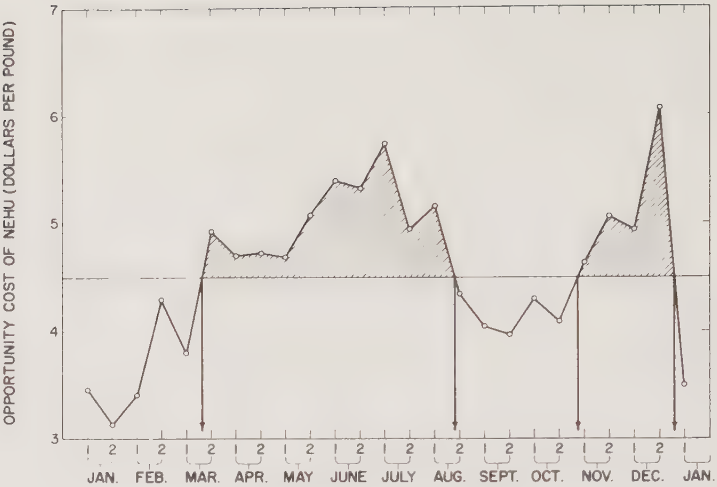


Figure 4.—Relationship between average ex-vessel aku price and average skipjack tuna landings, based on biweekly statistics averaged over 1968-73.

Figure 5.—Seasonal pattern in opportunity cost of nehu, averaged over 1968-73, showing the feasible period for bait substitution generated by a scheme producing bait at a cost of $4.50/lb used.



the industry, unmeasured by the opportunity cost analysis, due to the rise in aku production. We may define the "best" system as the one generating the greatest increase in the fleet's profits.

To compute the catch revenues and net costs under each alternative scheme we first determine the corresponding distribution of work days (potential fishing days). This partitioning is accomplished by solving the system of equations

$$DT = ADF + ADB$$
$$BD = \alpha ADF - \beta ADB$$

where DT = total work days during the feasible period,

BD = amount of bait delivered and used by the substitution scheme during the feasible period,

α = amount of bait used in a day of aku fishing,

β = amount of bait obtained in a day of baiting (after initial mortality),

ADF = adjusted days fishing,

ADB = adjusted days baiting.

It is easy to show that the only nontrivial solution is

$$ADF = \frac{(DB + \beta DT)}{(\alpha + \beta)}$$

and

$$ADB = DT - ADF$$

The coefficients α and β are different for each feasible period (delivery season) and are computed from current statistics.

With ADB and ADF determined for a particular substitution scheme we can compute the net gain to the aku fleet as

$$\text{GAIN} = P_2 - P_1,$$

$$= (ADF - DF)\left\{\pi CR\left(\frac{B}{DF}\right) - k_1\left(\frac{B}{DF}\right)\left(\frac{DT}{DB}\right) - (k_1 - k_2)\right\},$$

$$= \text{Additional catch revenue} - \text{Costs of bait purchase} - \text{Additional net operating costs}$$

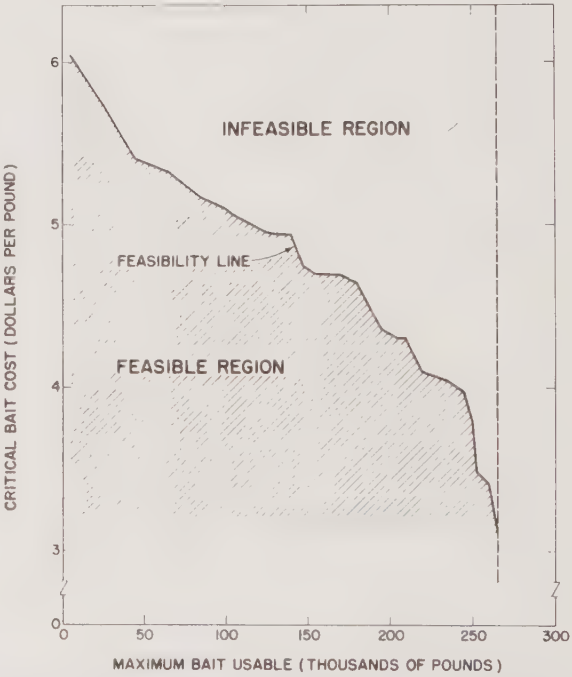


Figure 6.—Feasibility line for judging bait substitution schemes. Schemes falling in the infeasible region produce more bait than can be used in the feasible period generated. The feasibility curve is also the demand curve for bait in the Hawaiian aku fishery.

ASSUMPTIONS AND UNCERTAINTIES

The foregoing sections have outlined three basic steps in establishing the feasibility of bait substitution schemes in the Hawaiian aku fishery. These are: 1) determine the seasonal pattern of the opportunity cost of nehu; 2) compute the boundaries of the feasible region, i.e., determine the feasibility line; and 3) for each alternative substitution scheme in the feasible set compute the corresponding gain to the aku fleet.

At each step a number of critical assumptions are made. Basically there are two classes of assumptions. The first class involves assumptions made in estimating the feasibility line, i.e., the opportunity cost of nehu and the potential bait usage rate. One such assumption e.g., concerns the size of a bucket of nehu. In estimating the opportunity cost of nehu we must convert the bait usage rate from buckets per day, the reported unit, to pounds per day. The standard conversion rate used historically and in this paper is 7 pounds of nehu per bucket. On the other hand we may choose to adopt a figure of 14.2 lb/bucket on the strength of recent sampling (Hida and Wetherall 1977). If this is done, the estimates of potential bait usage will increase by 103%, while estimates of the catch rate and hence the opportunity cost of nehu will be cut by one-half.

The second category of assumptions concerns details of specific substitution schemes considered in step (3)—items such as expected survival rates during bait transport, reproductive capacity of cultured bait, attractiveness of the alternative bait relative to the standard bait, and so on. Survival rates during transport and similar parameters are likely to be fairly well known from experiments and trial runs of the system. However, other important assumptions, such as those concerning the relative attractiveness of the alternative bait, tend to be accepted uncritically. That they become tacit assumptions is a dangerous pitfall in a feasibility analysis—they must be made explicit, and tested if possible.

In the case of relative attractiveness of the standard bait and its alternatives, it is common at the outset to assume equivalence, but in the absence of concrete evidence supporting this assumption. a range of values should be explored. For a first-cut assessment, a reasonable range can be established without field trials. On theoretical grounds, e.g., we may expect that attractiveness of a pound of chummed bait is proportional to the surface area of the bait. The surface area of an individual fish is roughly proportional to the square of its length, so fish for fish the larger northern anchovy may be more attractive than nehu. But there are more nehu per pound. The number per pound is the reciprocal of average individual weight, and this is proportional to the cube of length. Combining the "surface area" and "number per pound" considerations, and noting the similarity in morphometrics between the two species, we may conclude that pound for pound the relative attractiveness of nehu versus anchovy is inversely proportional to the ratio of their average lengths. That is, if the anchovy are twice as long, they are only half as attractive as nehu, pound for pound. While this analysis ignores possible differences in behavior and other important characteristics (Yuen 1977), it provides useful guidance for setting limits to the assumption on relative attractiveness.

The effect of average size on relative attractiveness is important not only in choosing between two alternative bait species, but also in finding the best size for any particular species. Where a range of bait sizes is available, an optimum size surely exists. Of course, determining the optimum will involve consideration not only of relative attractiveness but also other factors such as carrying capacity of baitwells for different sized fish, relative production costs, and so on.

Finally, implicit in the earlier discussion on evaluating alternative systems is the assumption that the entire amount of bait delivered is purchased and used by the aku fishermen (or accepted and used, in the case of a vertically integrated system). If this is not the case, and some bait dies or is discarded between the time of delivery and fishing, then two important results follow. First, the unit cost of bait under the scheme is increased. If the fraction of bait ultimately used is μ, the cost will increase by a factor of $\frac{1}{\mu}$ over the unit cost under full utilization. Second, the net gain to the fleet will not be as great. The correct result is found using the equation given above for GAIN, but substituting a more general expression for adjusted days fishing,

$$ADF(\mu) = \frac{(\mu BD + DT)}{(\alpha + \beta)}$$

and, if the bait is purchased at cost, an amended cost figure, $\frac{k_3}{\mu}$.

It is clear, then, that in judging bait substitution schemes no meaningful conclusions can be drawn without a careful consideration of assumptions underpinning the analysis. Quoting appropriately from Chapman (1965), ". . . if far reaching assumptions are made, then strong conclusions are reached. But if these assumptions are not accepted, then the whole structure built upon sand collapses."

ACKNOWLEDGMENTS

A draft of this paper was kindly reviewed by Moheb A. Ghali and Richard S. Shomura. I thank them, and also Richard N. Uchida for his informative discussions.

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The Pacific Tuna Pole-and-Line and Live-Bait Fisheries

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ABSTRACT

The pole-and-line and live-bait fisheries of the eastern, central, and western Pacific Ocean are reviewed, including landing trends of tunas and catch and effort statistics on the fisheries for the tuna baitfishes. It was estimated that landings of tuna by the live-bait, pole-and-line fisheries contributed about 35% of the total Pacific landings of tunas in 1970. Also included were gross comparisons of the relative effectiveness of the live bait used in the various fisheries and discussions of the factors that may affect the relative effectiveness. The mean catch of tuna in metric tons per metric ton of bait was estimated at 7.5 in the eastern Pacific, 9.8 in the Japanese fishery, and 23.1 in the Hawaiian pole-and-line fishery. Thus, in terms of the catch per unit of bait, the Hawaiian fishery was 3.1 times more efficient than the eastern Pacific fishery and 2.3 times more efficient than the Japanese pole-and-line fishery.

The Japanese anchovy, *Engraulis japonicus*, is the most important bait species used in the Japanese pole-and-line fishery. In the eastern Pacific fishery the more important bait species are the anchoveta, *Cetengraulis mysticetus*; northern anchovy, *E. mordax*; California sardine, *Sardinops caerulea*; Galapagos sardine, *S. sagax*; and southern anchovy, *E. ringens*. The Hawaiian skipjack tuna fishermen primarily use nehu, *Stolephorus purpureus*.

INTRODUCTION

The total landings of skipjack tuna, *Katsuwonus pelamis*; yellowfin tuna, *Thunnus albacares*; albacore, *T. alalunga*; and bigeye tuna, *T. obesus*, in the Pacific Ocean by all methods of fishing amounted to an estimated 702,600 t in 1970 (FAO 1971). It is estimated that of these total landings, 243,800 t were made by the pole-and-line fishing method using live bait. The landings by the pole-and-line fisheries represent about 35% of the total landings by all methods of fishing.

Purse seine fishing for tropical tunas in the eastern Pacific was not very successful during the years prior to 1957. During the period from 1931 to 1956 the fishery for yellowfin tuna and skipjack tuna was dominated by bait boats, and purse seiners produced less than 15% of the yellowfin tuna and about 13% of the skipjack tuna catch (Broadhead 1962). However, beginning in 1957, the development of several technological innovations helped to reverse the trend, so that by 1960, the purse seine fleet had displaced the bait boats as the major producer of tunas in the eastern Pacific Ocean (Alverson 1963).

Because of the success of purse seining as practiced in the eastern Pacific, attempts were recently made to utilize this method on skipjack tuna in the central Pacific ([Hawaii.] Division of Fish and Game and Bumble Bee Seafoods [1970?]). The experiments were partially successful. In the western Pacific the Japanese have also been trying this method (Watakabe 1970) but, like the Hawaiian experiments, they have not been an unqualified success (Hester and Otsu 1973). Thus, in spite of its highly successful use in the eastern Pacific, the purse seine method with all of its technological advancements still requires more improvement for successful use in the central and western Pacific. Consequently, pole-and-line fishing with live bait is still the dominant method of fishing for tunas at the surface in the central and western Pacific.

Although the fishery in the eastern Pacific is now dominated by purse seiners, pole-and-line fishing with live bait is still practiced. In 1972 there were 52 bait boats of U.S. registry operating in the eastern Pacific (IATTC 1973). In the western Pacific, the Japanese have a highly viable pole-and-line fishery for skipjack tuna and albacore. And in the central Pacific a small but important pole-and-line fishery for skipjack tuna exists in Hawaii.

The purpose of this report is to present descriptions of the pole-and-line and live-bait fisheries in the eastern, central, and western Pacific, to review the historical catch and effort statistics on the fisheries for tuna baitfishes, and to compare the relative effectiveness of the live bait used in the three representative fisheries mentioned above. We will also discuss the factors that may contribute to the relative effectiveness of bait in terms of the volume of tuna produced. The material for this paper was taken almost entirely from published papers and reports.

EASTERN PACIFIC FISHERY

As noted earlier, the eastern Pacific tropical tuna fishery at present is essentially a purse seine fishery but,

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prior to 1957, was predominantly a live-bait fishery. In 1948, of 118,752 t of skipjack tuna and yellowfin tuna landed by the eastern Pacific fleet, about 84% was caught by bait boats. By 1960, the proportion had dropped to about 40% as the "purse-seine revolution" launched a mass conversion of bait boats to seiners. In recent years, only about 10% of the tunas has been landed by bait boats.

The geographical extent of the eastern Pacific pole-and-line fishery for yellowfin and skipjack tunas, as given by Shimada and Schaefer (1956) is shown in Figure 1. This figure shows the extent of the fishery in 1954, and includes purse seiner operations. During the period prior to 1957, when the bait boats dominated the fishery, they ranged over a large area in the eastern Pacific, from Cedros Island, Mexico (lat. 28°N), to northern Peru (about lat. 10°S). Except for the offshore islands and banks, most of the tuna catches were made within a few hundred miles of the coastline (Alverson 1959). By 1963, as noted in the Annual Report of the Inter-American Tropical Tuna Commission (IATTC 1964), many of the larger bait boats had been converted to purse seiners and the remaining bait boat fleet was composed of vessels of less than 170 tons capacity which generally operated north of the Gulf of Tehuantepec (ca. lat. 15°N).

Alverson (1959) discussed the seasonal nature of the eastern Pacific fishery for yellowfin and skipjack tunas during the period from 1952 to 1955. During this 4-yr period the catches of yellowfin tuna and particularly skipjack tuna were poorest in the first quarter (January-March). The catches of both species improved in the second quarter and continued good in the third. Alverson believed that the fourth quarter would have been the best of the year had it not been for some economic factors, including strikes and slow unloading of vessels. It should be pointed out that the seasonal nature of the fishery as described above is an oversimplification. The geographical extent of the fishery is large and there are variations in abundance in various localities in any one season.

Beginning in 1966, because of the use of increasingly efficient purse seine vessels, management procedures were implemented on the yellowfin tuna. These procedures were in the form of restricted fishing periods. In recent years the season of unrestricted fishing has grown increasingly short and in 1972 was only about 4 mo (IATTC 1972). The skipjack tuna stocks in the eastern Pacific are still not under management.

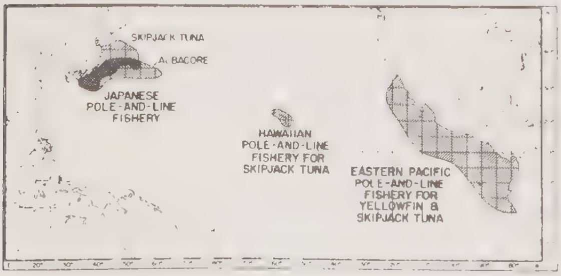
SKIPJACK TUNA
ALBACORE
JAPANESE POLE-AND-LINE FISHERY
HAWAIIAN POLE-AND-LINE FISHERY FOR SKIPJACK TUNA
EASTERN PACIFIC POLE-AND-LINE FISHERY FOR YELLOWFIN & SKIPJACK TUNA

Figure 1.—Geographical location of the eastern Pacific, Hawaiian, and Japanese pole-and-line fisheries for tunas.

Bait Species Utilized

Nearly all the species of fish used as live bait in fishing for tunas in the eastern Pacific belong to the herring and anchovy families (Alverson and Shimada 1957). These fishes are usually small and school in shallow waters nearshore. In 1946-58, the anchoveta, *Cetengraulis mysticetus*, composed from 29.6 to 59.5% of the bait taken by the bait boats, but in 1959, it represented only 21.8% of the bait taken (Table 1). In 1960-69, the percentage of the catch consisting of anchoveta varied between 10.0 and 34.9% and averaged slightly more than one-fifth of the bait catch.

Among the qualities that made anchoveta highly desirable as a baitfish were its wide distribution, wide range of temperature tolerance, and ability to survive for long periods in the baitwells (Alverson and Shimada 1957).

A species that has become important only since the 1960's is the northern anchovy, *Engraulis mordax*. Table 1 shows that in 1946-60, less than 19% of the catch consisted of this species. In 1961-69, however, the northern anchovy gradually replaced the anchoveta as the predominant bait species (Fig. 2). While the 1961 catch of anchoveta composed 32.5% of the total bait catch, the northern anchovy and California sardine, *Sardinops caerulea*, represented 27.5% and 16.3% of the total bait catch, respectively, both relatively higher than in 1960 (IATTC 1962). By 1963, the northern anchovy had become the predominant species in the catch. The change from anchoveta to northern anchovy as the predominant bait species reflected the shift in the composition of the tuna fleet from one consisting predominantly of bait boats to one of purse seiners. As noted earlier, after the mass conversion from bait boats to seiners, the majority of the remaining bait boats were small vessels of under 150-ton capacity that usually fished north of the Gulf of Tehuantepec where northern anchovies were more common.

Baiting Areas

Alverson and Shimada (1957) listed the anchoveta, the California sardine, the Galapagos sardine, *Sardinops sagax*, the northern anchovy, and the southern anchovy, *Engraulis ringens*, as the most important baitfishes in the eastern Pacific. The principal baiting areas for these five major species are given in Table 2 and their locations are shown in Figure 3.

Catch and Baiting Effort

Alverson and Shimada (1957) noted that the fishery for baitfish, a subordinate but integral part of the eastern Pacific tuna fishery, is not predisposed to the easy collection of reliable catch records. The only source of information is the detailed accounts of baiting kept by fisher-

Table 1.—Estimated amounts, in thousands of scoops and percentages of kinds, of baitfishes taken from 1946 to 1969 by bait boats (excludes bait caught by vessels fishing out of Latin American ports and that by a few small vessels fishing out of California).

	Anchoveta, *Cetengraulis mysticetus*		California sardine, *Sardinops caerulea*		Galapagos sardine, *Sardinops sagax*		Northern anchovy, *Engraulis mordax*		Southern anchovy, *Engraulis ringens*		California sardine and northern anchovy mixed		Herring, *Opisthonema, Harengula*		Salima, *Xenocys jessiae*		Miscellaneous and unidentified		Total catch
Year	Scoops	%	Scoops	%	Scoops	%	Scoops	%	Scoops	%	Scoops	%	Scoops	%	Scoops	%	Scoops	%	Scoops
1946	398	29.6	389	28.9	28	2.1	132	9.8	—	—	203	15.1	23	1.7	126	9.4	45	3.3	1,344
1947	836	39.5	405	19.1	97	4.6	141	6.7	—	—	250	11.8	62	2.9	259	12.2	66	3.1	2,116
1948	964	32.3	416	13.9	753	25.2	147	4.9	—	—	349	11.7	42	1.4	217	7.3	95	3.2	2,983
1949	1,079	39.3	514	18.7	570	20.7	138	5.0	—	—	217	7.9	40	1.5	117	4.3	73	2.6	2,748
1950	1,700	47.6	318	8.9	959	26.9	239	6.7	—	—	187	5.2	45	1.3	32	0.9	90	2.5	3,570
1951	1,708	63.5	366	13.6	130	4.8	143	5.3	—	—	13	0.5	137	5.1	118	4.4	76	2.8	2,691
1952	2,542	59.5	286	6.7	596	14.0	577	13.5	—	—	53	1.2	124	2.9	51	1.2	40	0.9	4,269
1953	1,618	37.2	413	9.5	1,145	26.3	814	18.7	36	0.8	168	3.9	88	2.0	31	0.7	36	0.8	4,349
1954	1,820	46.3	203	5.2	590	15.0	604	15.4	553	14.1	65	1.7	49	1.2	23	0.6	20	0.5	3,927
1955	1,321	51.0	541	20.9	247	9.6	159	6.2	214	8.3	9	0.4	49	1.9	21	0.8	25	0.9	2,586
1956	1,667	45.6	362	9.9	152	4.2	594	16.2	355	9.7	38	1.0	368	10.1	27	0.7	95	2.6	3,658
1957	2,070	55.8	290	7.8	38	1.0	547	14.8	410	11.1	30	0.8	193	5.2	17	0.5	112	3.0	3,707
1958	1,515	34.0	601	13.5	141	3.2	736	16.5	1,169	26.3	57	1.3	102	2.3	16	0.4	110	2.5	4,447
1959	649	21.8	290	9.7	110	3.7	190	6.4	1,484	49.8	30	1.0	75	2.5	24	0.8	128	4.3	2,980
1960	416	34.9	110	9.2	82	6.9	212	17.8	214	17.9	6	0.5	64	5.4	15	1.2	74	6.2	1,193
1961	211	32.5	106	16.3	8	1.2	179	27.5	88	13.5	2	0.3	26	4.0	14	2.2	16	2.5	650
1962	123	29.6	89	21.4	34	8.2	110	26.5	25	6.0	2	0.5	16	3.9	7	1.7	8	1.9	414
1963	56	23.2	19	8.0	29	12.1	101	41.8	—	—	8	3.3	22	9.2	1	0.4	5	2.2	241
1964	37	16.5	54	24.1	74	33.0	41	18.3	--	—	1	0.4	8	3.6	4	1.8	5	2.2	224
1965	34	11.0	41	13.3	33	10.7	147	47.7	—	—	2	0.7	34	11.0	10	3.3	7	2.3	308
1966	49	17.3	68	23.9	22	7.7	106	37.3	—	—	3	1.1	24	8.4	9	3.2	3	1.1	284
1967	61	25.6	56	23.5	14	5.9	94	39.5	—	--	—	-	8	3.4	4	1.7	1	0.4	238
1968	37	13.7	54	19.9	18	6.6	148	54.6	—	—	1	0.4	10	3.7	2	0.7	1	0.4	271
1969	25	10 0	40	16.1	10	4.0	153	61.5	—	—	1	0.4	16	6.4	0	0.0	4	1.6	249

men in their logbooks. Based on data collected from about 85% of the bait boats based in California ports, scientists at the IATTC have been able to estimate the amounts and kinds of baitfish taken by all California bait boats operating in the eastern Pacific.

Table 3 gives the annual catches of all species of baitfish caught by bait boats in 1946-69. The annual catches, measured in scoops holding 4 kg (8 lb) of bait (Shimada and Schaefer 1956), varied from 224,000 scoops in 1964 to 4,447,000 scoops in 1958. At the height of the bait boat era, annual catches of 3.5-4.0 million scoops were not uncommon. From 1946 to 1959, when the bait boats dominated the fishery, the annual catches averaged 3,241,000 scoops. In 1960-69, the average annual catch reached only 407,000 scoopes, about one-eighth of the pre-1960 catches.

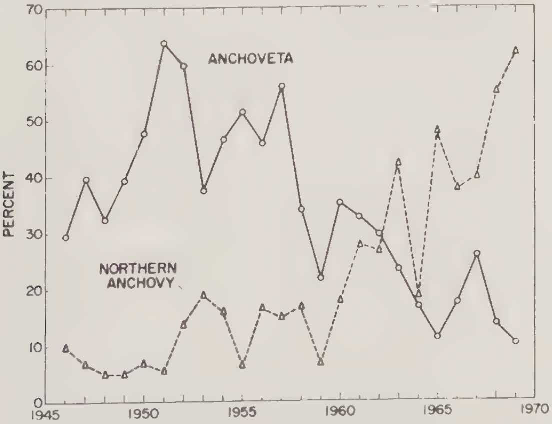

Figure 2.—Percentage of anchoveta and northern anchovy in the baitfish catches of bait boats in the eastern Pacific tuna fishery, 1946-69.

Data on baiting effort are not usually published in the annual reports of the IATTC. For 1939-51, Peterson (1956) gave the recorded and estimated catches and baiting effort for anchovetas, herring, and other miscellaneous species in the Gulf of Nicoya (Table 4). Alverson and Shimada (1957) also published catch and baiting effort data giving the catch per standard day's baiting, estimated total catch, and calculated baiting intensity for anchovetas in several of the major baiting grounds. Their data are reproduced in Table 5.

HAWAIIAN FISHERY

The Hawaiian pole-and-line fishery for skipjack tuna is conducted within 90 mi of the main islands of Hawaii, Oahu, Maui, Kauai, and Molokai (Fig. 1). Skipjack tuna are taken throughout the year, but the bulk of the catch is made between May and September. Smaller fish from 1.8 to 2.3 kg (4 to 5 lb) are taken all year long, but during the months of peak catches large fish ranging from 5.9 to 11.3 kg (13 to 25 lb) are also taken. These larger fish constitute a large percentage by weight of the total annual catch (Uchida 1967).

Unlike the eastern Pacific tuna fishery, where the demand for live bait has declined since 1960, catches of live bait are becoming increasingly important in other areas

Table 2.—Major baiting localities for five of the most important bait species used by eastern Pacific bait boats (compiled from Alverson and Shimada 1957).

Species	Major baiting grounds	Season
Anchoveta *Cetengraulis mysticetus*	Ranges from central Baja California to northern Peru. Important baiting grounds are Almejas Bay in Baja California, Guaymas and Ahome Point in the Gulf of California, and Gulf of Fonseca and Gulf of Panama in Central America.	Caught in appreciable numbers at one season or another throughout the year.
California sardine *Sardinops caerulea*	Ranges from San Diego, Calif., along outer coast of Baja California and along western side of Gulf of California as far north as Santa Catalina Island. Important grounds are at Cedros Island, Santa Maria Bay, and Magdalena Bay in Baja California and San Jose Island in Gulf of California.	July to November.
Galapagos sardine *Sardinops sagax*	Galapagos Islands.	September through February.
Northern anchovy *Engraulis mordax*	From San Diego, Calif., to Cape Falso at southernmost extremity of Baja California. Important grounds are at Turtle Bay, Santa Maria Bay, and Magdalena Bay; San Quentin Bay and Abreojos Point in some years.	June through November.
Southern anchovy *Engraulis ringens*	Cape Blanco, Peru to about lat. 10°S.	September through January.

of the Pacific. The Hawaiian fishery for skipjack tuna is small compared with those in the eastern and western Pacific, but it is the only commercial pole-and-line fishery in the midst of what is believed to be a vast resource of skipjack tuna extending throughout the tropical and subtropical central Pacific.

Bait Species Utilized

In Hawaii, a small, fragile anchovy locally called nehu, *Stolephorus purpureus*, is captured day and night and constitutes roughly 95% of the baitfish used for skipjack

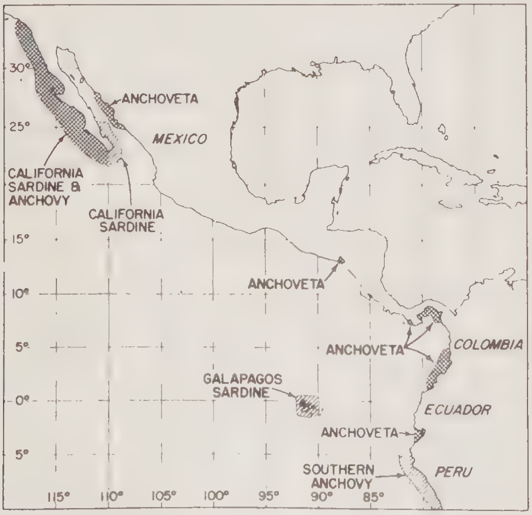

Figure 3.—Principal baiting areas of the California live-bait fishery for yellowfin and skipjack tunas (from Alverson and Shimada, 1957).

Table 3.—Annual catches of live bait in the eastern Pacific (all species), Hawaiian (nehu), and Japanese (anchovy) fisheries for bait.

Year	Eastern Pacific[1] (scoops)	Hawaii[2] (buckets)	Japan[3] (metric tons)
1946	1,344,000	25,860	—
1947	2,116,000	30,750	—
1948	2,983,000	42,036	—
1949	2,747,000	39,558	—
1950	3,570,000	39,638	—
1951	2,691,000	40,491	—
1952	4,269,000	29,807	—
1953	4,349,000	37,682	—
1954	3,927,000	43,737	—
1955	2,586,000	49,712	—
1956	3,653,000	40,864	—
1957	3,707,000	30,638	18,468
1958	4,447,000	33,303	18,109
1959	2,980,000	37,637	16,304
1960	1,193,000	22,849	15,916
1961	650,000	37,092	15,604
1962	414,000	34,256	15,526
1963	241,000	32,670	16,067
1964	224,000	30,606	14,915
1965	308,000	36,352	27,568
1966	284,000	31,603	22,262
1967	238,000	31,832	18,320
1968	271,000	35,535	20,771
1969	249,000	30,096	21,606
1970	—	33,596	21,264
1971	—	42,098	20,848
1972	—	38,970	—

[1] Data for 1946-69 are from IATTC (1956, 1962, 1968, 1970).

[2] Data for 1946-53 are from Yamashita (1958); data for 1954-72 are unpublished data courtesy of the Hawaii Division of Fish and Game. (Data for 1960-72 have been adjusted after correcting errors in catch reports.)

[3] Data from [Japan.] Ministry of Agriculture and Forestry, Statistics and Survey Division (1958-62, 1964-73).

Table 4.—Recorded and estimated catches in scoops and number of days of fishing for anchovetas, *Cetengraulis mysticetus*, and other baitfishes taken by California-based tuna clippers from the Gulf of Nicoya from 1939 to 1951. On the left side of the table are the recorded or actual catches and actual number of days of fishing obtained from logbooks made available to the commission by a segment of the fleet. Estimates for the entire fleet are shown to the right. Also shown is the average catch of anchovetas per day of fishing (from Peterson 1956).

	Recorded catch and days fishing					Estimated catch and days fishing					
Year	Anchoveta	Herring	Miscellaneous	Total	No. days fishing	Anchoveta	Herring	Miscellaneous	Total	No. days fishing	Catch of anchovetas per day of fishing
1939	23,902	—	—	23,902	49.0	220,756	—	—	220,756	486.0	454
1940	1,958	—	—	1,958	12.0	25,310	—	—	25,310	152.5	166
1941	11,704	—	—	11,704	58.0	89,590	—	—	89,590	449.5	199
1942	2,438	—	—	2,438	9.5	19,249	—	—	19,249	74.5	258
1943	7,600	—	—	7,600	16.0	54,688	—	—	54,688	116.0	471
1944	2,917	—	—	2,917	18.5	23,539	—	—	23,539	143.0	165
1945	6,148	357	—	6,505	47.0	29,282	2,156	—	31,438	232.5	126
1946	35,408	58	667	36,133	115.0	90,190	554	5,848	96,592	323.5	279
1947	23,420	4,647	1,821	29,888	233.5	57,536	14,978	4,984	77,498	628.0	92
1948	3,473	7,920	5,272	16,665	82.5	7,123	15,090	10,432	32,645	163.5	44
1949	683	53	—	736	11.0	1,157	89	—	1,246	19.5	59
1950	—	4,181	1,547	5,728	26.0	—	6,615	2,449	9,064	51.5	0
1951	—	—	—	—	2.0	—	—	—	—	2.0	0

Table 5.—Catch per standard day's baiting, estimated total catch, and calculated fishing intensity for anchovetas in Almejas Bay, Guaymas, Ahome Point, Gulf of Fonseca, and Gulf of Panama, 1946-54 (Alverson and Shimada 1957).

	Almejas Bay			Guaymas			Ahome Point			Gulf of Fonseca			Gulf of Panama		
Year	Catch per standard day's baiting scoops/class 4 day	Estimated total catch in scoops	Calculated fishing intensity, in class 4 days	Catch per standard day's baiting scoops/class 4 day	Estimated total catch in scoops	Calculated fishing intensity, in class 4 days	Catch per standard day's baiting scoops/class 4 day	Estimated total catch in scoops	Calculated fishing intensity, in class 4 days	Catch per standard day's baiting scoops/class 4 day	Estimated total catch in scoops	Calculated fishing intensity, in class 4 days	Catch per standard day's baiting scoops/class 4 day	Estimated total catch in scoops	Calculated fishing intensity, in class 4 days
1946	283.4	28,847	102.0	520.0	184,192	354.0	404.8	47,705	110.5	334.7	39,896	119.0	300.0	5,999	20.0
1947	289.4	100,594	347.5	424.9	325,503	766.0	313.8	149,186	475.5	220.6	36,020	163.5	355.6	143,445	403.5
1948	410.8	218,728	532.5	—	0	0	502.0	331,539	660.5	29.9	972	32.5	456.7	395,563	886.0
1949	291.4	236,293	811.0	76.4	949	12.5	751.6	278,166	370.0	118.1	3,336	28.0	679.1	513,973	757.0
1950	583.6	498,558	854.3	819.9	481,470	587.0	676.8	81,830	121.0	355.0	18,669	52.5	355.7	183,378	515.5
1951	526.1	246,077	467.5	618.6	433,088	700.0	711.5	419,033	589.0	478.8	172,062	359.5	597.7	204,479	352.0
1952	451.5	374,115	828.5	627.8	584,706	931.5	360.6	72,460	201.0	526.2	286,148	544.0	616.8	925,689	1,501.0
1953	599.4	347,016	578.9	748.9	355,580	475.0	753.3	165,491	219.5	148.9	5,435	36.5	421.5	623,290	1,478.5
1954	613.8	101,754	166.0	829.0	439,903	530.5	892.1	114,133	128.0	527.0	47,793	90.5	530.8	760,564	1,433.0

tuna fishing. Nehu is preferred above all others by the skipjack tuna fishermen because it possesses most of the qualities of a good baitfish. But nehu is also extremely fragile and during seining and transferring from seines to baitwells, many fish are injured and die of their injuries. Annually, an average of about 22% of the nehu die before they can be used in tuna fishing.

Other small fish are also used for bait. Almost all the remainder of the bait catch in Hawaii is composed of silverside or iao, *Pranesus insularum*, and small round herring or piha, *Spratelloides delicatulus*.

Baiting Areas

Nearly 79% of the live bait captured in the Hawaiian Islands comes from the island of Oahu. Two of the major baiting grounds are Kaneohe Bay and Pearl Harbor, which together contribute about 71% of the State's bait catch. Other areas of less importance are Kalihi-Keehi Lagoon and Honolulu Harbor.

On the neighboring islands, baiting grounds appear to have diminished in importance, probably due to a reduction in the number of vessels based there. Good baiting areas on Maui are the Maalaea Bay region (including Kihei), Lahaina, and Kahului. On the island of Hawaii, the vessels usually catch bait in Hilo Bay, Kawaihae, Mahukona, and Kona. Kauai has Port Allen, Nawiliwili, Hanalei, and Hanapepe as baiting areas. Infrequent attempts are made to bait at Lanai and at Kaunakakai, Molokai.

Catch and Baiting Effort

In Hawaii, bait catches are reported to the State on the same form as that used for reporting skipjack tuna catches. The form has undergone several revisions over

Table 6.—Catch, effort, and catch per effort in the fishery for nehu in Hawaii, 1960-72.

	Nehu - day			Nehu - night			Nehu - day and night			Other species - day and night			Totals		
Year	Catch (buckets)	Effort days (no.)	Catch per day (buckets)	Catch (buckets)	Effort nights (no.)	Catch per night (buckets)	Catch (buckets)	Effort days and nights (no.)	Catch per effort (buckets)	Catch (buckets)	Effort days and nights (no.)	Catch per effort (buckets)	Annual catch (buckets)	Effort days and nights (no.)	Catch per effort (buckets)
1960	15,735	1,001	15.7	3,069	408	7.5	2,489	297	8.4	1,556	145	10.7	22,849	1,851	12.3
1961	25,309	940	26.9	7,804	639	12.2	2,150	130	16.5	1,829	102	17.9	37,092	1,811	20.5
1962	23,544	823	28.6	7,819	623	12.6	1,585	126	12.6	1,308	83	15.8	34,256	1,655	20.7
1963	21,832	817	26.7	7,731	851	9.1	1,414	95	14.9	1,693	124	13.6	32,670	1,887	17.3
1964	18,454	774	23.8	9,618	1,003	9.6	1,547	82	18.9	987	63	15.7	30,606	1,922	15.9
1965	19,972	839	23.8	14,251	1,424	10.0	1,142	50	22.8	987	52	19.0	36,352	2,365	15.4
1966	20,696	781	26.5	10,242	1,011	10.1	480	20	24.0	185	19	9.7	31,603	1,831	17.2
1967	22,432	740	30.3	9,201	914	10.1	—	–	—	199	12	16.6	31,832	1,666	19.1
1968	30,148	1,055	28.6	4,911	544	9.0	96	4	24.0	380	17	22.4	35,535	1,620	21.9
1969	25,650	870	29.5	4,164	374	11.1	65	2	32.5	217	25	8.7	30,096	1,271	23.7
1970	30,332	1,017	29.8	2,654	288	9.2	112	3	37.3	498	24	20.8	33,596	1,332	25.2
1971	38,786	1,334	29.1	2,776	288	9.6	30	1	30.0	506	38	13.3	42,098	1,661	25.3
1972	36,503	1,171	31.2	2,187	206	10.6	30	1	30.0	250	15	16.7	38,970	1,393	28.0
Total	329,393	12,162		86,427	8,573		11,140	811		10,595	719		437,555	22,265	
Mean	25,338	936	27.1	6,648	659	10.1	928	68	13.7	815	55	14.8	33,658	1,71[illegible]	19.6

the years, but in all the various versions used, the fishermen have reported date of catch, locality, amount of bait caught, and amount used. More recently, the forms have also included spaces for recording zero-catches, the amount of bait that died, and the amount of bait left over after fishing. Unlike commercial fish catches that are published and distributed monthly by the Hawaii Division of Fish and Game, bait catches are not published.

The annual catches of live bait in the Hawaiian Islands are given in Table 3 (see also Uchida 1977). In 1946-72, the bait catches ranged from a low of 22,849 buckets in 1960 to 49,712 buckets in 1955 and averaged 35,528 buckets. Yamashita (1958) estimated that a bucket holds about 3.2 kg (7 lb) of nehu.

Data on catch, baiting effort, and catch per effort of nehu taken in 1960-72 are given for day and night baiting in Table 6. Also included in the table are nehu catches for which the bait reports gave no time of capture, and catches of other species. Data on effort have not been corrected for variations in bait catches due to differences in efficiency among the different-sized fishing vessels.

Of particular interest were the opposite trends of day and night catches of nehu. Table 7 gives the baiting effort expended during the day and at night and their percentages of the total effort in 1960-72. A distinct pattern was obvious. Whereas 71% of the baiting effort in 1960 was expended in day operations, only 37% was expended during the day in 1965. A change in the ratio of day to night baiting in 1966, however, carried day effort back to the 1960 level and by 1972, 85% of the baiting effort expended was during the day. The change in emphasis in day and night baiting in 1960-72 is reflected in the catches of day and night bait shown in Figure 4.

JAPANESE POLE-AND-LINE FISHERY

In Figure 1 can be seen the geographical extent of the Japanese pole-and-line fishery for skipjack tuna and albacore. The figure for skipjack tuna was taken from

Table 7.—The amounts, percentages, and means of day and night effort expended in the bait fishery for nehu in Hawaii, 1960-72.

	Baiting effort				
Year	Day	Percent	Night	Percent	Day and night total effort
1960	1,001	71	408	29	1,409
1961	940	60	639	40	1,579
1962	823	57	623	43	1,446
1963	817	49	851	51	1,668
1964	774	44	1,003	56	1,777
1965	839	37	1,424	63	2,263
1966	781	44	1,011	56	1,792
1967	740	45	914	55	1,654
1968	1,055	66	544	34	1,599
1969	870	70	374	30	1,244
1970	1,017	78	288	22	1,305
1971	1,334	82	288	18	1,622
1972	1,171	85	206	15	1,377
Total	12,162		8,573		20,735
Mean	936		659		1,595
Percent		59		41	

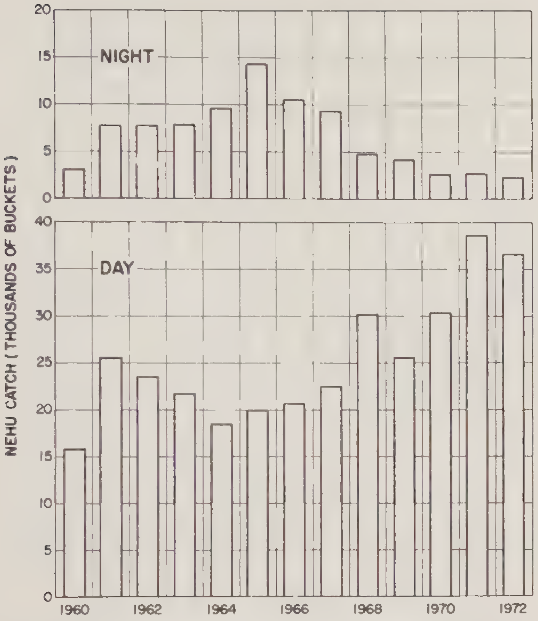

Figure 4.—Annual catches in the day and night fishery for nehu in Hawaii, 1960-72.

Rothschild and Uchida (1968) and that of albacore from Otsu and Uchida (1963). The albacore fishery extends over a thousand miles offshore whereas the skipjack tuna fishery tends to be more coastal.

Generally, over 75% of the annual catch of skipjack tuna is made from May through September. However, variations to this general rule occur in the sector of the fishery north of about lat. 35°N. Here the fishery may begin as early as April or as late as July and may end as early as August or as late as October. The seasonal development of the albacore fishery is somewhat similar to that of the skipjack tuna. Small catches of albacore are usually made in March or April and between the latter part of April and the end of May the first large catches are made. The season peaks in June and by the end of July the season is virtually over. Fishing for skipjack tuna and albacore are interrelated in that most of the pole-and-line fleet seek out skipjack tuna except during the brief period when the albacore are most abundant (Van Campen 1960).

Japanese vessels harvest about two-thirds of the world's skipjack tuna catch, which annually reaches about 300,000 t (Kawasaki 1972). The bulk of the catch is made by the traditional method using pole-and-line and live bait, although since 1964 the Japanese fishing industry has been actively engaged in experimental fishing with purse seines to capture skipjack tuna (Watakabe 1970; Yabe 1972).

Despite the fact that the skipjack tuna fishery has a long history and is well established among Japanese commercial fishing enterprises, pressure has been mounting in recent years to expand and develop this fishery even further. In 1970, realizing that the deep-swimming larger tunas were already being fished at or near the maximum level by the far ranging longline fleet, the Japanese Fisheries Agency turned its attention to further development of the skipjack tuna resource in southern waters (Suisan Shūhō 1973). Automatic fishing poles installed on pole-and-line fishing vessels proved successful and will probably help in significantly reducing future manpower needs (Suzuki Tekkojo Kabushiki Kaisha 1970). But skipjack tuna fishing has not developed as rapidly as expected. Two of the most pressing needs at present are to develop methods of transporting live bait to distant fishing grounds and to capture live bait in areas outside foreign territorial waters (Suda 1972).

Bait Species Utilized

About 97% of the live bait used in Japan today is an anchovy, *Engraulis japonicus*, known as katakuchi iwashi in Japanese (Katsuo-Maguro Nenkan 1971). Imamura (1949) listed various other species that have been used as bait in the past. Among them were maiwashi or sardines, *Sardinops melanosticta*; muroaji or scad, *Decapturus muroaji*; and the juveniles of masaba or mackerel, *Scomber japonicus*. Cleaver and Shimada (1950) published an extensive list of fishes that were used as live bait in the pre-World War II fisheries in Japan, the Ryukyu Islands, and the South Seas (Table 8).

Katakuchi iwashi was not always the predominant bait species in Japan. Imamura (1949) listed maiwashi as the predominant species in the immediate post-World War II period. Maiwashi, he stated, was more resistant to injury and excitement, whereas katakuchi iwashi was resistant to oxygen deficiency.

Baiting Areas

There are more than 60 baiting areas for anchovy in Japan (Katsuo-Maguro Nenkan 1971). These areas are given in Table 9. During a visit to Japan in 1974, one of the coauthors (T. Otsu) made firsthand observations on the bait fisheries in Shizuoka Prefecture (Ajiro, Usami), Oita Prefecture (Tsukumi), and Nagasaki Prefecture (Segawa). The areas are representative of the Kanto and Kyushu baiting areas (central and southwestern Japan, respectively). Following are some of the observations made during that visit.

There is considerable demand for live bait in Shizuoka Prefecture, which is the leading skipjack tuna fishing prefecture in Japan. Because the prefectural baiting areas periodically experience shortages, several bait-transport vessels are now in operation carrying fish purchased from Kyushu baiting areas to Shizuoka Prefecture. Most of the anchovy in Shizuoka Prefecture are taken by one-boat or two-boat purse seines. In addition to the seiners, a baiting unit includes a fish-finder vessel, a small scouting vessel, and a tugboat to tow the bait receivers to and from the fishing grounds.

Table 8.—Some baitfishes used by the Japanese skipjack tuna fishery (from Cleaver and Shimada 1950).

Scientific name	Common names
Japan and Ryukyu Islands	
Amia notata	kurohoshi-tenjikudai, ufumi
A. truncata	ufumi
Atherina bleekeri	tōgoro-iwashi
A. tsurugae	aoharara, gin-isō-iwashi
Beryx decadactylus	gasagasa, nanyō-kinmedai
Caesio coerulaureus	saneera, shimamuro-gurukun
C. digramma	gurukun
Caranx djeddeba	gatsun
Engraulis japonicus	katakuchi-iwashi, segurō-iwashi, tarekuchi-iwashi
Harengula zunasi	sappa
Lutjanus vaigiensis	mochinogwa, okifuefuki
Pomacentrus anabatoids	hichigwa, hikigwa
Pseudupeneus sp.	himeji
Sardinella mizun	mizun
Sardinia immaculata	hoshinashi-iwashi, shiira
S. melanosticta	ma-iwashi
Scomber japonicus	ōsabanoko, saba
South Seas	
Amia sp.	akadoro
Apogon sp.	akadoro
Archamia bleekeri	atohiki-tenjikudai
Atherina sp.	kokera, tobi-iwashi, tōgoro-iwashi
Atherina valenciennesii	nanyō-tōgoro-iwashi
Caesio chrysozonus	akamuro, gurukun, saneera, umeiro
Caranx leptolepis	aji
C. malabalicus	shima-aji
Caranx sp.	aji, gatsun
Chilodipterus sp.	akadoro
Dascyllus trimaculatus	montsuki
Decapterus russelli	akamuro
Decapterus sp.	muro, shima-muro
Gazza equulasformis	hiiragi
Harengula molluciensis	ma-iwashi, nanyō-ma-iwashi
Labracoglossa argentiventris	takabe
Mullus sp.	ojisan
Sardinella leiogaster	mangurōbu-iwashi
Scomber kanagurta	saba
Sphyraena obtusata	kamasu
Spratelloides delicatulus	ao-iwashi, baka, nanyō-kibinago, shiira
Trachurops crumenophthalma	me-aji
Trachurus japonicus	ma-aji
Upeneus sp.	ojisan
Upeneus tragula	yomehimeji
Upenoides sp.	ojisan
Stolephorus heterolobus	nanyō-katakuchi-iwashi, tarekuchi
S. japonicus	bakasako, kibiko-iwashi, sururu

Table 9.—Baiting areas for anchovy in Japan (Katsuo-Maguro Nenkan 1971).

Prefecture	Baiting areas
Iwate	Miyako, Yamada, Tanohama, Oozuchi, Ofunato, Hirota, Ohno, Takada
Miyagi	Kesennuma, Shizukawa, Takenoura, Onagawa, Sameura, Makinohama, Momoura, Koamigura
Chiba	Tateyama, Tomiura, Katsuyama, Hoda, Kisarazu
Kanagawa	Koajiro, Shimoura, Sajima, Hayama
Shizuoka	Ajiro, Usami, Tago, Mito, Heda, Enoura
Mie	Goza, Hamajima, Shukutaso, Kamimae, Shiroura, Sugari, Mikiura, Nagashima
Wakayama	Kushimoto, Tanabe
Kochi	Asakawa, Shukumo
Ehime	Uwajima
Oita	Tsukumi, Saeki
Miyazaki	Takashima
Saga	Imari
Nagasaki	Sasebo, Imafuku, Hatashita, Takashima, Higashihama, Omodaka, Tawaragaura, Nakura
Kumamoto	Ushibuka, Miyaura, Yokoura
Kagoshima	Ooneshime, Furue, Umigata, Sakurajima, Yamakawa, Oura

The bait fishery at Tsukumi in Oita Prefecture is one of the important baiting areas in Kyushu. It is operated strictly for vessels from outside prefectures since Oita Prefecture does not have a skipjack tuna fishery of its own. Vessels from Shizuoka, Kochi, and Miyazaki Prefectures, among others, come here to purchase bait. The baiting fleet in Tsukumi consists of two 7-ton catcher boats (seiners), a one-boat seiner, a 2-ton lightboat, a transport, and a tugboat.

Bait from the bait fishery in an area in Segawa Bay, Nagasaki Prefecture, is reported to be of excellent quality. It is known as "Sasebo bait" and is taken in Omura Bay, an enclosed bay located between Nagasaki City and Sasebo City. Vessels from various prefectures come here to make purchases. Fishing is largely by purse seining but about a third of the catch is made by beach seining, a method which reportedly produces superior bait.

Catch and Baiting Effort

Data on the amount of anchovy caught and sold as live bait may be found in the Annual Report of Catch Statistics on Fishing and Aquiculture ([Japan.] Ministry of Agriculture and Forestry, 1958-62, 1964-73). There are, however, no statistical data on the amount of effort expended in catching bait.

Japanese pole-and-line vessels usually purchase bait from bait fishermen. It has been estimated that roughly 10% of the anchovy catch in Japan is actually marketed for use as live bait (Katsuo-Maguro Nenkan 1971). Data on total catch of anchovy and the amount of anchovy sold as live bait in three principal regions of Japan show that in 1968, out of a total catch of 225,348 t of anchovy, 24,097 t or 10.7% was sold as live bait.

In 1957-71, the catch of anchovy as live bait varied from 14,915 t in 1964 to 27,538 t in 1965 (Table 3). The average amount of anchovy sold as live bait annually was 19,103 t.

Although the amount of anchovy sold as live bait is reported in metric tons, the actual unit of measurement that the bait fishermen use in selling bait is the bucket. As in Hawaii, the amount of bait per bucket is quite variable. For example, the bucket in the Kanto (central Japan) baiting areas holds an average of 3.4 kg of baitfish whereas that in the Sanriku (north of Ibaragi Prefecture including the Tohoku area) and the Shikoku-Kyushu areas averages 6-7 kg or more of baitfish. In order to compare bait production from the eastern and western

Pacific, we converted the eastern Pacific catches to metric tons, using 3.6 kg of bait per scoop. The average annual eastern Pacific catch of live bait during the period when bait boats dominated the fishery (1946-59) was 11,760 t, roughly two-thirds of the Japanese bait production.

LANDINGS OF TUNA

The estimated landings of yellowfin and skipjack tunas by bait boats in the eastern Pacific are shown in Figure 5. These estimates were obtained by using the data on the percentage of the total landings made by bait boats as given in the annual reports of the IATTC and the California landings data provided by Frey (1971). The most striking feature of Figure 5 is the sudden drop in the landings of both species starting in 1959. This sudden decline was caused, of course, by the conversion of a large number of the bait boats to purse seiners. It can be seen that, during the period from 1950 to 1958, the bait boats landed between about 37,000 and 68,000 t of yellowfin tuna and 33,000 and 62,000 t of skipjack tuna. In more recent years the bait boat landings have stabilized at a low level with only small fluctuations.

The landings of tuna in the Japanese pole-and-line fishery from 1958 to 1971 are shown in Figure 6. The category "others" in this figure includes yellowfin, bigeye, and bluefin, *Thunnus thynnus*, tunas; and frigate mackerels, *Auxis*. The Japanese pole-and-line fishery appears to be stabilized in that there are no apparent upward or downward trends in the landings. Skipjack tuna landings fluctuated from 70,423 to 212,985 t during this period. The landings of albacore varied between a low of 8,729 and a high of 52,957 t. The landings of other tunas ranged from 9,081 to 28,342 t.

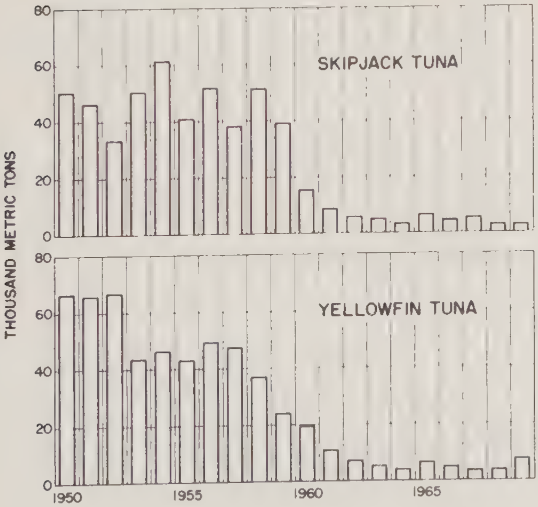

Figure 5.—Estimated landings of yellowfin and skipjack tunas by California-based bait boats in the eastern Pacific fishery.

The Hawaiian pole-and-line fishery also did not show any positive or negative trends (Fig. 7). The landings ranged from a low of 2,679 to a high of 7,329 t during the period from 1950 to 1972.

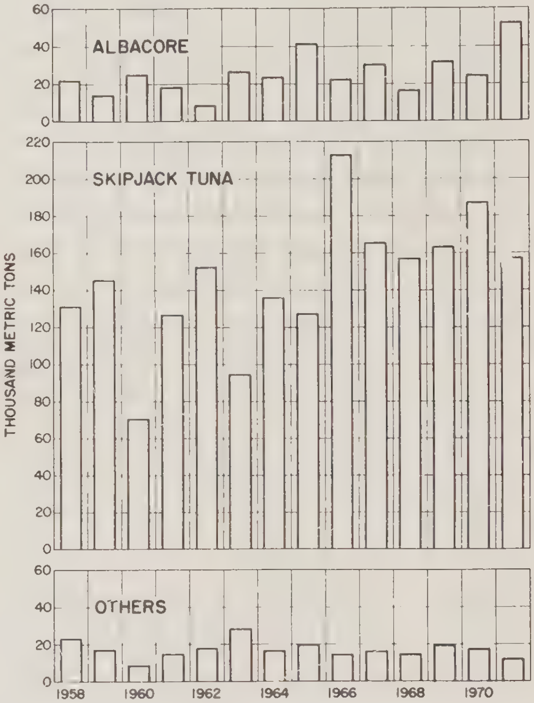

Figure 6.—Landings of tuna in the Japanese pole-and-line fishery.

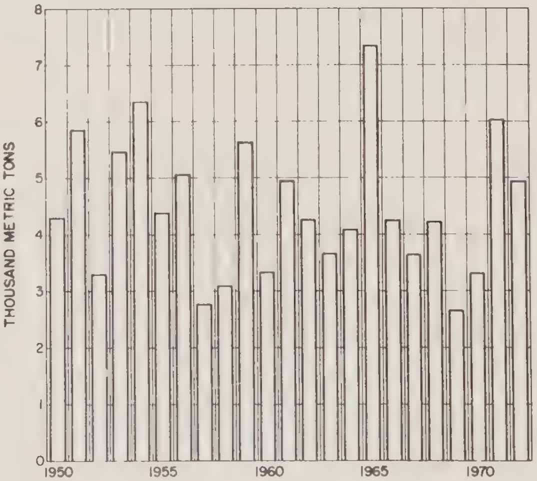

Figure 7.—Landings of skipjack tuna in the Hawaiian pole-and-line fishery.

RELATION OF LANDINGS TO FLEET SIZE

It is interesting to determine, roughly, how the total landings are related to number of boats and to catch per boat, especially in the eastern Pacific where a large number of bait boats were converted to purse seiners. The combined total catch of yellowfin and skipjack tunas, the number of bait boats, and the catch per boat in the eastern Pacific are shown in Figure 8. As noted earlier the conversion of bait boats to purse seiners caused a decline in the number of bait boats in the eastern Pacific tuna fleet. This resulted directly in a decline in the total landings of tuna by the bait boats and also a decline in the mean catch per boat, probably related to the resultant size composition of the bait boat fleet after the mass conversion. It has been shown in the eastern Pacific fishery for tunas that the success of fishing is related to vessel size, the larger vessels being the more efficient (Shimada and Schaefer 1956). Recent data in the annual reports of the IATTC on the size composition of the bait boat fleet show very few boats larger than 182 t (200 short tons) capacity after 1959 (Table 10). Therefore it appears that the eastern Pacific bait boat fleet has been reduced not only in number but also in efficiency.

Similar data on the total catch of tuna, number of boats, and the catch per boat from 1958 to 1971 in the Japanese pole-and-line fishery are shown in Figure 9. The total catch includes all the tunas taken by pole and line and the boats include only those larger than 20 t. Live-bait boats smaller than 20 t number in the thousands but these vessels primarily catch frigate mackerel and contribute only a small amount to the skipjack tuna and albacore landings (Van Campen 1960).

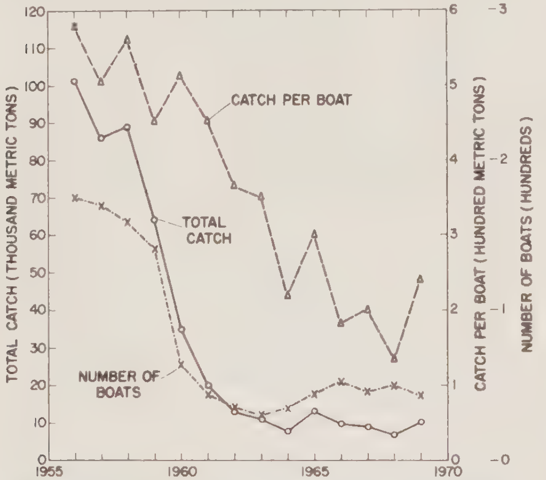

Figure 8.—Total catch of yellowfin and skipjack tunas, number of bait boats, and catch per boat in the eastern Pacific pole-and-line fishery.

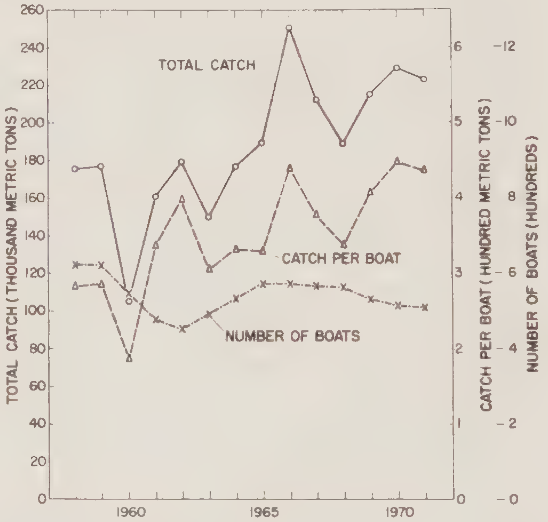

Figure 9.—Total catch of tunas, number of boats, and catch per boat in the Japanese pole-and-line fishery. (Original data from [Japan.] Ministry of Agriculture and Forestry. Statistics and Survey Division, 1960-1973.)

Table 10.—The number of bait boats based in U.S. ports (including Puerto Rico) in the pole-and-line fishery in the eastern Pacific (from IATTC 1961, 1966, 1971).

Year	Capacity in metric tons and short tons (in parentheses)						Total
	<46.4 (51)	46.4-90.9 (51-100)	91.8-181.8 (101-200)	182 -272.7 (20 -300)	273.6-363.6 (301-400)	364.5 (≥ 401)	
1956	12	11	43	66	32	11	175
1957	11	11	43	60	35	10	170
1958	12	8	35	56	36	11	158
1959	13	8	31	46	33	10	141
1960	10	7	21	11	17	3	69
1961	11	4	17	1	11	0	44
1962	13	4	12	1	6	0	36
1963	13	4	11	2	0	0	30
1964	16	5	11	2	1	0	35
1965	21	7	12	3	1	0	44
1966	25	9	11	5	2	0	52
1967	21	9	10	4	2	0	46
1968	23	11	10	4	2	0	50
1969	17	12	9	4	1	0	43

Because catches of boats smaller than 20 t, but not number of boats, were included in the computations, the catches per boat as shown in Figure 9 are probably higher than the actual catches. However, this should not mask any trends that may be present.

The number of boats in the Japanese pole-and-line fishery has fluctuated between 451 and 623 from 1958 to 1971. Although, as it was pointed out earlier, there was no trend apparent in the landings of the various tuna species, it appears that the total tuna landings are increasing. The catch per boat also appears to be on a slight upward trend. There has been a change in the size composition of the Japanese pole-and-line fleet in that since 1967 the number of vessels in the 200- to 500-t class has been increasing (Table 11). If size is also related to efficiency in the Japanese pole-and-line fishery, then the increase in the catch per boat could be accounted for by the increasing number of larger boats in the fleet.

The number of boats in the Hawaiian pole-and-line fishery has been declining steadily since 1950 (Fig. 10). It is interesting that in spite of this the landings have not declined correspondingly. The catch per boat showed large annual fluctuations, but appeared to be at a higher level after 1963 than before. Except for the addition of one new vessel in December 1971, the composition of the Hawaiian fleet has remained unchanged for many years. Thus, although the new addition to the Hawaiian fleet is a larger vessel with a greater fish-carrying capacity and range than the average Hawaiian boat, this fact alone cannot account for the apparent increase in efficiency. Among other things, a change in fishing techniques has been suggested as a factor in the improved efficiency of Hawaiian pole-and-line vessels (Uchida 1967).

Table 11.—The number of pole-and-line boats in various size categories (metric tons) in the Japanese fishery (from [Japan.] Ministry of Agriculture and Forestry 1959-62, 1964-73).

Year	20-30	30-50	50-100	100-200	200-500	>500	Total
1958	19	68	239	273	24	—	623
1959	18	80	234	262	26	—	620
1960	11	98	179	229	28	—	545
1961	19	122	132	178	26	—	477
1962	13	173	111	126	28	—	451
1963	33	207	111	112	29	—	492
1964	40	251	103	106	32	—	532
1965	14	284	91	148	35	—	572
1966	14	285	71	167	34	—	571
1967	12	284	54	173	41	—	564
1968	5	271	60	170	54	1	561
1969	4	244	71	156	53	—	528
1970	2	218	91	140	61	—	512
1971	2	163	133	129	83	—	510

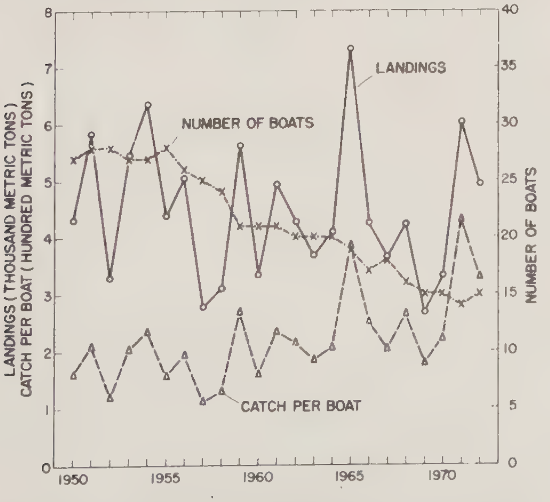

Figure 10.—Landings of skipjack tuna, number of boats, and catch per boat in the Hawaiian pole-and-line fishery. (Original data from Hawaii Division of Fish and Game.)

BAIT AND TUNA CATCHES

The catch of tuna and the amount of bait used in the Japanese pole-and-line fishery from 1957 to 1971 are shown in Table 12. Although skipjack tuna and albacore are the most important species of tuna caught in the pole-and-line fishery, as noted earlier appreciable amounts of other species are also taken with live bait. These include frigate mackerel and bluefin, bigeye, and yellowfin tunas (listed under "others" in Table 12). In analyzing the relative effectiveness of the Japanese anchovy in the pole-and-line fishery the total catch of all species should be considered. This must be done because although the statistics published by the Japanese Government lists all the species caught by the pole-and-line method, no breakdown is given on the amount of bait expended to catch each species. In addition to the tunas, species of mackerel are actively fished with live bait and pole and line. These catches will not be included in the discussion, but it should be borne in mind

Table 12.—Catch of tunas and bait (metric tons) in the Japanese pole-and-line fishery (from [Japan.] Ministry of Agriculture and Forestry, Statistics and Survey Division 1958-62, 1964-73.)

Year	Skipjack tuna	Albacore	Others[1]	Total	Japanese anchovy[2]	Tuna catch per unit of bait
1957	92,156	49,500	20,675	162,331	18,468	8.8
1958	131,441	22,190	22,778	176,409	18,109	9.7
1959	145,447	14,252	17,058	176,757	16,304	10.8
1960	70,428	25,156	9,081	104,665	15,916	6.6
1961	127,011	18,636	14,914	160,561	15,604	10.3
1962	152,387	8,729	18,111	179,227	18,526	9.7
1963	94,757	26,420	28,342	149,519	16,067	9.3
1964	136,081	23,858	16,827	176,766	14,915	11.8
1965	127,436	41,491	19,821	188,748	27,568	6.8
1966	212,985	22,830	14,718	250,533	22,262	11.2
1967	165,492	30,481	16,431	212,404	18,320	11.6
1968	157,340	16,597	15,021	188,958	20,771	9.1
1969	163,455	31,912	19,641	215,008	21,606	10.0
1970	187,438	24,263	17,391	229,092	21,264	10.8
1971	157,380	52,957	12,327	222,664	20,848	10.7
Total				2,793,642	286,548	
n				15	15	
Mean				186,243	19,103	9.7

[1] Includes *Auxis*, bluefin, bigeye, and yellowfin tunas.

[2] *Engraulis japonicus*.

that an undetermined amount of bait and effort is expended towards the catch of these nontuna species.

The total landings of tuna from 1957 to 1971 in the Japanese pole-and-line fishery ranged from 104,665 to 250,533 t with an expenditure of 14,915 to 22,262 t of bait. The tuna catch per unit of bait (CPUB) ranged from 6.6 to 11.8 t per metric ton of bait. The mean values for the 14-yr period were 186,243 t for the total annual catch of tuna, 19,103 t for the annual catch of anchovy, and 9.7 t of tuna per metric ton of bait for the mean annual CPUB.

Table 13 gives the estimated landings of skipjack and yellowfin tunas and the amount of bait caught from 1950 to 1969 by bait boats based in California ports. The bait data were given in terms of "scoops" in the IATTC annual reports, and these were converted to metric tons.

The total bait boat landings of skipjack and yellowfin tunas ranged from 6,811 to 117,369 t and averaged 54,602 t. The total bait catch ranged from 813 to 16,138 t and averaged 7,304 t. The CPUB of yellowfin and skipjack tunas ranged from 5.5 to 12.2 t per metric ton of bait and averaged 7.5 t per metric ton of bait.

As noted earlier, several different species of fish are used as bait in the eastern Pacific bait boat fishery. However, there is nothing in the literature on a comparison of the relative effectiveness of the various species of bait used in this fishery. Although figures are available on the catch of baitfishes by species (Table 1), no figures are available on the catch of tunas by the use of the various species of bait. Thus the CPUB figures given in Table 13 are based on the total catch of all species of bait.

The catch of skipjack tuna and the amount of bait caught from 1950 to 1972 in Hawaii are given in Table 14. The bait catch statistics provided by the Hawaii Division of Fish and Game, which are given in terms of buckets, were converted to metric tons using a factor of 5.4 kg (12 lb) per bucket. In the past, the bucket was assumed to be equivalent to about 3.2 kg (7 lb) of fish (Yamashita 1958). However, more recent data indicate that this figure is an underestimate (T. S. Hida, Southwest Fisheries Center, Honolulu, HI 96812, pers. commun.).

Table 13.—Estimated landings (metric tons) of yellowfin and skipjack tunas by bait boats based in California ports.

Year	Landings				Tuna catch per unit of bait
	Yellowfin tuna	Skipjack tuna	Total	Catch bait	
1950	66,655	50,714	117,369	12,956	9.0
1951	66,000	46,626	112,626	9,766	11.5
1952	67,018	33,435	100,453	15,492	6.5
1953	43,797	50,374	94,171	15,782	6.0
1954	46,524	61,235	107,759	14,251	7.6
1955	43,157	41,041	84,198	9,384	9.0
1956	49,363	51,940	101,303	13,257	7.6
1957	47,524	38,403	85,927	13,453	6.4
1958	37,173	51,511	88,684	16,138	5.5
1959	24,332	39,215	63,547	10,814	5.9
1960	19,664	15,690	35,354	4,329	8.2
1961	10,965	8,900	19,865	2,359	8.4
1962	7,257	5,972	13,229	1,502	8.8
1963	5,468	5,215	10,683	874	12.2
1964	3,988	3,656	7,644	813	9.4
1965	6,604	6,649	13,253	1,118	11.8
1966	4,812	4,728	9,540	1,031	9.2
1967	3,692	5,587	9,279	864	10.7
1968	3,748	3,063	6,811	983	6.9
1969	7,409	2,936	10,345	904	11.4

The skipjack tuna catch ranged from 2,679 to 7,324 t from 1950 to 1972. The catch of bait ranged from 124 to 270 t and the skipjack tuna CPUB ranged from 16.3 to 37.0 t per metric ton of bait. The mean values were 4,478 t of skipjack tuna, 194 t of bait, and 17.2 t of skipjack tuna per metric ton of bait.

The relative effectiveness of the bait used in these fisheries in terms of CPUB is summarized in Table 15. It can be seen that the mean annual CPUB for the Hawaiian fishery at 23.1 was higher than the Japanese and eastern Pacific fisheries. In terms of the CPUB then, the Hawaiian pole-and-line fishery is 3.1 times more efficient than the eastern Pacific fishery and 2.3 times more efficient than the Japanese fishery.

Table 14.—Catch of nehu and skipjack tuna (metric tons) in the Hawaiian pole-and-line fishery.[1]

Year	Nehu catch	Skipjack tuna catch	Skipjack tuna catch in metric tons per metric ton of nehu
1950	216	4,312	20.0
1951	220	5,863	26.6
1952	162	3,308	20.4
1953	205	5,470	27.1
1954	238	6,360	26.7
1955	270	4,397	16.3
1956	222	5,050	22.7
1957	167	2,781	16.6
1958	181	3,100	17.1
1959	205	5,631	27.5
1960	124	3,338	26.0
1961	202	4,942	24.3
1962	186	4,271	22.7
1963	178	3,674	20.6
1964	166	4,093	23.5
1965	198	7,329	37.0
1966	172	4,257	24.8
1967	173	3,647	21.0
1968	193	4,228	21.9
1969	164	2,679	16.3
1970	183	3,314	18.2
1971	229	6,023	26.3
1972	212	4,930	23.1

[1] Original data courtesy Hawaii Division of Fish and Game.

Table 15.—The relative effectiveness of live bait used in the eastern Pacific, Japanese, and Hawaiian pole-and-line fisheries.

Area and period	Mean annual catch of tuna (metric tons)	Mean annual catch of bait (metric tons)	Mean annual catch of tuna per unit of bait (metric tons)
Eastern Pacific (1950-69)	54,602	7,304	7.5
Japan (1957-71)	186,243	19,103	9.7
Hawaii (1950-72)	4,478	194	23.1

FACTORS AFFECTING CPUB

The CPUB in terms of the weight of tuna caught in a pole-and-line fishery can be affected by many variables including the size and species of fish caught, the number of men fishing, the number of fish in a unit weight of bait, and, less directly, the apparent abundance of the fish caught.

The size of the fish would affect the CPUB in that, assuming that fish up to a certain maximum size, i.e., one-pole size fish, are caught at the same rate, the catch in weight would be greater if the fish caught were larger. If the fish are so large as to require a two-pole rig, then the effective fishing power would be reduced because it would require two men to bring in one fish. However, it may happen that the fish are large enough to balance out or even exceed the difference caused by the loss of fishing power in using a two-pole rig. In the eastern Pacific fishery, one pole is used on fish up to 13.6 kg (30 lb). For fish from 13.6 to 27.2 kg (30 to 60 lb) two-pole rigs are used. With fish larger than 27.2 kg, a three-pole rig is used (Godsil 1938). In the Japanese pole-and-line fishery albacore fishing is done with two-pole rigs and one-pole rigs are used on skipjack tuna (Van Campen 1960).

Another important variable affecting the CPUB is the number of fish in a unit weight of bait. Obviously, the size of the fish will affect the number in a unit weight of bait: the larger the fish, the fewer per unit. Presumably, the greater the number of fish per unit weight of bait, the greater would be the "fishing power." The length-frequency distribution of the baitfishes used in the three fisheries is shown in Figure 11. For the eastern Pacific fishery, the length distribution of two of the more important baitfishes, the anchoveta and the northern anchovy, is shown. If it is assumed that these size distributions are representative of the bait in the three fisheries, it can be seen that the bait used in the Hawaiian fishery is generally the smallest and that used in the eastern Pacific the largest. The Japanese anchovy is intermediate in size between the Hawaiian and the eastern Pacific baitfishes. It can be deduced, then, that the fishing power of a unit weight of bait in the Hawaiian fishery is greater than that in the eastern Pacific and Japanese pole-and-line fisheries.

Finally, the apparent abundance of the tunas in any one year may have an influence on the mean annual

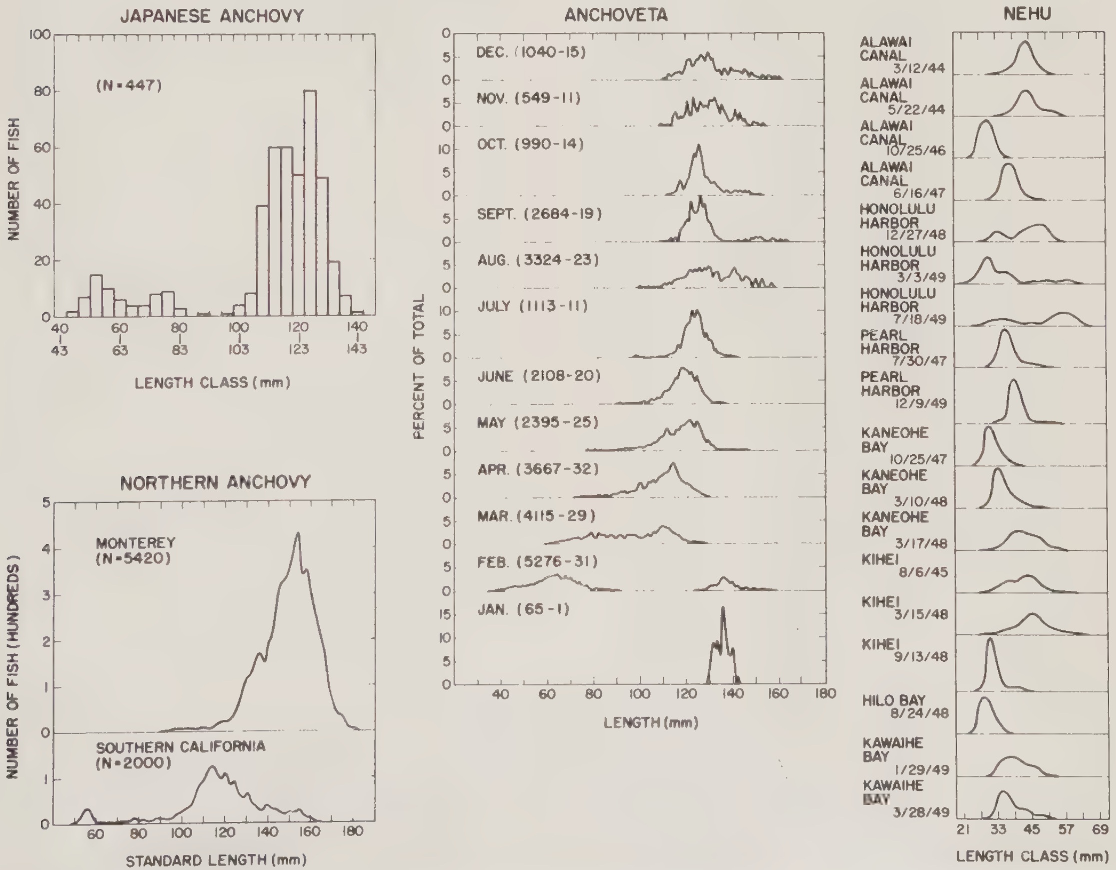

Figure 11.—Length-frequency distribution of Japanese anchovy, anchoveta, northern anchovy, and nehu. (From Clark and Phillips 1952; Tester and Hiatt 1952; Mie Prefectural Fisheries Experiment Station 1953; Howard and Landa 1958.)

CPUB: if the apparent abundance is higher, it may be expected that the mean annual CPUB will be greater. Figure 12 shows the relation between the mean annual CPUB and the mean annual apparent abundance for skipjack tuna in the Hawaiian fishery, and Figure 13 shows the mean annual CPUB and the mean annual apparent abundance of yellowfin and skipjack tunas in the eastern Pacific fishery. For the eastern Pacific figure, the apparent abundance is expressed in terms of the mean catch of yellowfin and skipjack tunas per day's fishing. The data for 1950-58 are based only on bait boat operations and the data for 1959-69 are means based on bait boat and purse seiner operations. The basic data were taken from the annual reports of the IATTC.

For the Hawaiian pole-and-line fishery figure, apparent abundance is simply represented by the total annual catch. Uchida (1967) found that the apparent abundance of skipjack tuna expressed as the catch per standard effective trip was correlated with the total catch of skipjack tuna from 1952 to 1962. He stated, therefore, that the total catch may be used as an index of apparent abundance during 1952-62. Although he cautioned against the use of the total catch as an index of apparent abundance for other years, we assumed that it was reliable for other years also.

It can be seen that CPUB was positively related to the apparent abundance of tuna in the eastern Pacific and the Hawaiian fisheries. In years when the apparent abundance was high the CPUB was also high. The coefficient of correlation was computed for the data for both fisheries. The results (eastern Pacific fishery, $r = 0.556$; df = 19; $P<0.01$; Hawaiian fishery, $r = 0.839$; df = 22; $P<0.01$) indicated that the mean annual CPUB was highly correlated with the apparent abundance of tuna.

Higgins (1966) examined the size distribution of the various tunas caught in the Pacific and noted fundamental differences in the sizes caught in the different areas. For example, he noted that larger skipjack tuna are caught around the Hawaiian Islands than in the eastern Pacific or near Japan. Obviously, it would be expected that differences in size would exist among the different species of tuna. The albacore caught by pole and line in the Japanese fishery are larger than the skipjack tuna caught by the same method. The yellowfin tuna taken by pole and line in the eastern Pacific are larger than the skipjack tuna. Thus CPUB is not only influenced by differences in sizes within the same species among the different fisheries, but also by the species of fish taken.

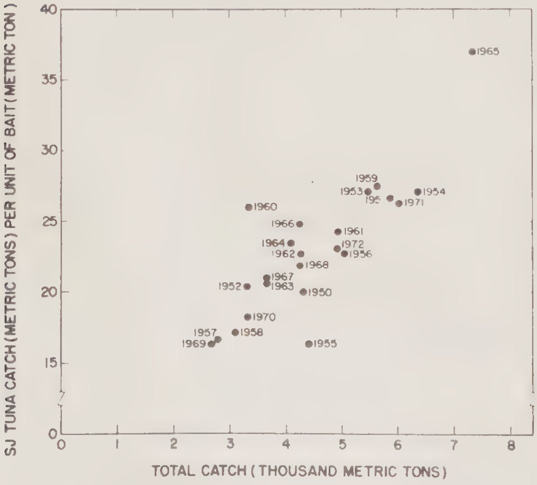

Figure 12.—Relation between total catch of skipjack tuna and catch per unit of bait in the Hawaiian pole-and-line fishery, 1950-72.

The number of men fishing per unit of bait expended also affects the CPUB. In the eastern Pacific fishery the size of the crew on a bait boat ranged from 12 to 20 men (Godsil 1938). The average number of crewmen on a Japanese pole-and-line boat ranged from 29 on 20- to 50-ton boats to 54 on 100- to 200-ton boats (Van Campen 1960). In the Hawaiian pole-and-line fishery from 1950 to 1960, Uchida (1967) indicated that, depending on the size of the vessel, an average of 6.7 to 10.4 fishermen fished on each trip. However, the relation between the number of men fishing and the amount of bait expended is not very clear. Generally, it is likely that more men fishing would require a greater use of bait. In the Japanese pole-and-line fishery bait is chummed at the stern, amidships, and forward (Van Campen 1960). In the eastern Pacific fishery, the smaller boats have one chummer and the larger ones usually have two (Godsil 1938). The Hawaiian pole-and-line boats usually have only one chummer.

SUMMARY

This report reviews the pole-and-line and live-bait fisheries of the eastern, central, and western Pacific Ocean including historical catch and effort statistics on

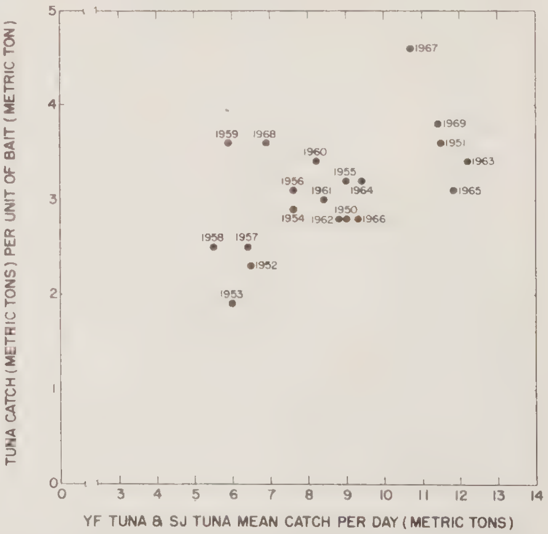

Figure 13.—Relation between the mean apparent abundance (catch per day's fishing) of yellowfin tuna and skipjack tuna and the catch per unit of bait in the eastern Pacific, 1951-69.

the fisheries for tuna baitfishes. Included in the report are comparisons on the relative effectiveness of the live bait used in the fisheries and a discussion of the factors that may contribute to the relative effectiveness.

Although the eastern Pacific fishery for yellowfin and skipjack tunas is now dominated by the purse seiners, bait boats are still active in that fishery. In Japan, the pole-and-line technique of catching albacore and skipjack tuna is still one of the important methods of fishing for tuna. And in Hawaii, the pole-and-line fishery for skipjack tuna is the most important fishery in the State.

In the Japanese pole-and-line fishery, the Japanese anchovy, *Engraulis japonicus*, is the most important bait species used. The more important bait species utilized in the eastern Pacific fishery are anchoveta, *Cetengraulis mysticetus*, northern anchovy, *E. mordax*, California sardine, *Sardinops caerulea*, Galapagos sardine, *S. sagax*, and southern anchovy, *E. ringens*. The Hawaiian skipjack tuna fishermen primarily use an anchovy called nehu, *Stolephorus purpureus*.

In the eastern Pacific it was seen that landings of yellowfin and skipjack tunas by the bait boats dropped suddenly starting in 1959 owing largely to the reduced number of bait boats in the fleet following the conversion of many of them to purse seiners. It was also seen that there was a downward trend in the catch per boat, which was attributed to a reduction in efficiency of the remaining bait boat fleet.

Landings of tuna by species in Japan did not show any important trends, although the total catch of all tuna species combined appeared to be increasing. The catch per boat also appeared to be on a slight upward trend. A change in the composition of the fleet by the addition of larger vessels may have contributed to the increasing catch per boat.

Landings of skipjack tuna in the Hawaiian pole-and-line fishery did not show any significant trends. However, the number of boats in the fleet has been steadily declining since 1950. The fact that the landings did not decline correspondingly suggested an improved efficiency in the operation of the Hawaiian pole-and-line fleet.

In terms of tuna catch per unit of bait, the Hawaiian fishery appeared to be the most efficient among the three tuna fisheries considered. Catch per unit of bait, however, is affected by many variables including size of tuna, number of men fishing, the number of fish in a unit weight of bait, and the apparent abundance of tuna.

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Desired Characteristics of a Bait for Skipjack Tuna, *Katsuwonus pelamis*

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ABSTRACT

Skipjack tuna, *Katsuwonus pelamis*, fishing in the central Pacific Ocean is largely dependent upon a limited supply of live baitfish, the nehu, *Stolephorus purpureus*. Experiments by the Honolulu Laboratory in a search for effective live-bait substitutes or supplements have resulted in the collection of much information on behavioral characteristics of the experimental baits. Characteristics of an effective skipjack tuna bait are: a tendency to flee towards the surface, elusiveness, a high light reflectance, a length of 2 to 6 cm, and the durability to survive in a baitwell.

INTRODUCTION

The only successful method of catching skipjack tuna, *Katsuwonus pelamis*, on a commercial scale in the clear waters of the central Pacific Ocean has been the pole-and-line method in which the skipjack tuna are attracted to the fishing boat with live bait. The major fishery for this species in the central Pacific Ocean is located in the Hawaiian Islands where the supply of nehu, *Stolephorus purpureus*, the principal bait species, is an important factor limiting the catch of skipjack tuna (June 1951). Since 1951 the Honolulu Laboratory of the National Marine Fisheries Service (then known as the Pacific Oceanic Fishery Investigations) has invested research effort in developing an artificial bait or finding a substitute species to augment the nehu.

As part of this effort studies were made of the perceptual abilities of skipjack tuna, their responses to various stimuli, their feeding responses at sea, and their responses to various species of live bait. For this paper on desired bait characteristics, I have tried to gather the relevant information from these studies.

SOURCE OF DATA

Beginning in 1957 (Strasburg and Yuen 1960), various underwater viewing facilities installed on the *Charles H. Gilbert*, a research ship of the Honolulu Laboratory, provided many opportunities to observe bait behavior and feeding responses of skipjack tuna under experimental conditions at sea. Many of the experiments were designed to compare the effectiveness of two different species as bait. In most cases nehu was one of the two species and was used as a control. With the exception of tilapia, *Tilapia mossambica*, which could be purchased, selection of experimental species was opportunistic; trials were made with whatever species could be obtained.

Because skipjack tuna at sea respond to live bait with a wide range of variability (Yuen 1959), experiments require much replication for reliable conclusions. Many of the experiments were not replicated sufficiently or not replicated at all because the desired bait was not sufficiently available, and, therefore, was not included in an earlier publication (Yuen 1969). The experiments, however, provided the opportunity to collect many observations on the behavioral characteristics of the experimental baits and the reaction of skipjack tuna to them. This collection of field notes is the major source of information on the desired characteristics of bait.

A total of 14 species (Table 1) was involved in the experiments. The species provided a wide range of characteristics in physical attributes as well as in behavior (also see Baldwin 1977). Some fish were shiny, others were dull; some were deep-bodied, others slender; some were fast, others slow; swimming motions were different.

CHARACTERISTICS

In the fishing operation for skipjack tuna the use of live bait serves two purposes. When the ship intercepts the

Table 1.—Species used in baitfish experiments in Hawaii.

Common Name	Scientific Name
Aholehole	*Kuhlia sandvicensis*
Iao	*Pranesus insularum*
Lae	*Scomberoides lysan*
Marquesan sardine	*Sardinella marquesensis*
Moi	*Polydactylus sexfilis*
Mullet	*Mugil longimanus*
Nehu	*Stolephorus purpureus*
Northern anchovy	*Engraulis mordax*
Oama	*Mulloidichthys* sp. (mix of several species)
Omaka	*Caranx mate*
Tabai	*Limia vittata*
Thread herring	*Opisthonema medirastre*
Threadfin shad	*Dorosoma petenense*
Tilapia	*Tilapia mossambica*

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school, bait is used to attract the skipjack tuna to the boat. Once the school is at the boat, the bait is used to hold the fish there so that they may be fished. A desirable characteristic for one function may not be a desirable characteristic for the other. For example, the most attractive bait should lure the skipjack tuna to the boat. On the other hand, if the bait is so attractive that the skipjack tuna always takes it in preference to the hook, it is not a desirable bait. In discussing the desired characteristics I shall consider both roles that the bait must play.

Behavior

Perhaps the most important characteristic to consider in examining the effectiveness of a bait is its behavior. The baits that were most effective in attracting the school to the boat were those that hastened back to the boat only after they were under attack by the skipjack tuna. Nehu, Marquesan sardine, *Sardinella marquesensis*, and mullet, *Mugil longimanus*, belong to this group. Most nehu gathered into a school before swimming away, almost always heading down. Mullet and Marquesan sardine swam away singly or in groups in no preferred direction. When attacked they all returned to the ship by following the wake.

Once the skipjack tuna are at the ship the most desirable bait behavior is initial diving and then fleeing towards the surface. With species that flee by diving only, results have been mixed. Catches have been good when the feeding frenzy of the skipjack tuna was great and each piece of bait was consumed as soon as it hit the surface. When the skipjack tuna were feeding lethargically or when the bait was especially elusive, diving bait took the skipjack tuna below the range of the hooks.

Some baits moved quickly to within a few centimeters of the hull of the boat for protection. These lost much of their effectiveness, because skipjack tuna did not seem to come closer to the ship than approximately a meter. Quickly moving the ship ahead to expose the bait was sometimes successful, but usually it was impossible to stop the ship before the skipjack tuna were beyond reach of the poles.

Iao, *Pranesus insularum*, did not move close to the ship but stayed exclusively at the surface. In general this behavior was effective in keeping the skipjack tuna within striking distance of the hooks. However, a common behavior of skipjack tuna is to move away from the boat and dive. In this circumstance, a bait that dives may attract the tuna back to the boat, whereas a bait that stays at the surface will not.

I have noticed that a bait that has a quick, short darting movement will excite skipjack tuna much more than a bait which swims in a slow steady manner. On occasion a slow steady bait has been completely ignored by the skipjack tuna. Excited skipjack tuna are more apt to take a hook than those that are not. An excited fish will snap at a hook unhesitatingly but an unexcited one may come up to a hook and veer away. A very quick and elusive bait can whip the school into a frenzy. It seems that excitement builds up with every unrewarded attack. If, however, the bait is very elusive and flees by diving, which is true with thread herring, *Opisthonema medirastre*, it can quickly draw the skipjack tuna down below the range of the hooks.

Size

Vision is the primary sense used by skipjack tuna during feeding. Therefore, large bait size would be expected to be desirable because the bait would then be detected at a greater distance. The largest size bait I have found in the stomach of a 60-cm skipjack tuna is 20 cm. A rough estimate of the maximum bait size for 70-cm skipjack tuna is 23 cm.

Water clarity and a high reflectance of the bait are important in the visibility range of the bait. Let us assume that water clarity limits the visible range to 50 m in extremely clear water. What size would the bait have to be to be seen? The visual acuity of skipjack tuna is about 0.18 (Nakamura 1968). The bait would have to be 8 cm long to be detected at 50 m. Under most circumstances 50 m is an unusual range so that 8 cm is as large as a bait needs to be.

If the bait behavior is such that it swims towards the ship when attacked, it can extend the effective range of the ship much more than a large bait can.

Another consideration in size of bait is the bait carrying capacity of boats. The number of fish to be caught with a load of bait depends on the number of pieces of bait. To the extent that the carrying capacity is fixed, one can carry a lot more pieces of small bait than large bait; therefore, a smaller bait is better.

Another argument against large bait is that large bait will satiate the skipjack tuna faster.

Survival

An obviously important characteristic for a bait is that it should be able to survive in a baitwell. The duration it needs to survive depends upon how far the fishing grounds are.

Flavor

Although aqueous extracts of skipjack tuna, shrimp, and squid have evoked positive and often violent responses from captive tuna, the use of these extracts at sea on "wild" skipjack tuna schools did not heighten their responses during feeding (Tester et al. 1954). From this I conclude that the taste or flavor of the bait is not important.

DISCUSSION AND SUMMARY

Yuen (1969), in discussing the effectiveness of water sprays in increasing the catch rate, felt that each skipjack tuna caught represented an error in discrimination by the skipjack tuna: a hook was mistaken for a live bait. Any strategem a pole-and-line fisherman uses to cause more mistakes by the skipjack tuna will increase his catch. He can make it more difficult for the skipjack tuna to discriminate between bait and hook by designing his hooks to look more like the bait or use sprays to distort vision. He can also cause the fish to be less discriminatory by exciting them with the use of a more elusive bait.

The most important characteristics of an effective bait are its behavioral characteristics. The bait should flee toward the boat when the predator is encountered. It should be elusive with fast, darting movements. It should be durable enough to survive in a baitwell. It should have a high light reflectance. It should be 2 to 6 cm long. The flavor of the bait is not important.

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NMFS RESEARCH ON PACIFIC BILLFISHES

You are at the Hawaiian International Billfish Tournament (HIBT), an annual event that transforms the community of Kailua-Kona into a beehive of activity. The fishing competition for billfishes and tunas is, of course, the core of it all. Since the beginning of HIBT 18 years ago, a host of activities has evolved around the competition. One of the more colorful of the satellite activities is the show that accompanies the weighing of the catch at the pier at the end of each day of fishing. There, at the pier, you witness emotions--suspense, elation, disappointment, excitement...;people--Miss Kona, Peter Fithian, Howard Kiyama, Judi Nakamaru, Richard Boone,Eric Tixier, Haku Baldwin, Paiboon Bencharit, Toshiro Mifune, RobynHall...;action--weighmasters weighing, judges judging, announcers announcing, photographers photographing, fish handlers handling fish....Away from center stage, between the scoreboard and the refreshment stand, other activity is going on. Two men are measuring, cutting, and examining the fish. Who are they? What are they doing that for? Answering those questions is what this article is about.

Ray Sumida and I have been the ones working over the fish in recent years. We are part of the staff of the Honolulu Laboratory. For those who have a pendhant Laboratory. For those who have a penchant for organizational structure, the Honolulu Laboratory is a part ot the Southwest Fisheries Center, which is a part of the National Marine Fisheries Service (NMFS), which is a part of the National Oceanographic and Atmospheric Administration (NOAA), wich is a part of the Department of the Commerce of the United States.

The purpose of the Honolulu Laboratory is to research fishery resources in the central Pacific Ocean to bring about optimal use of the resources. There are 10 tasks into which all of the research projects of the Honolulu Laboratory fit. One of them is structured to research on recreational fisheries and is appropriately called the Recreational Fisheries Task.

At HIBT, the measuring and examining of fish is our most visible activity. This work is for the purpost of gathering basic biological date on the billfishes. Data on lengths, weights, stomach contents, sex, species, and other noteworthy items are recorded. On occasion, material for special studies is also collected at the pier. An example of that is the collection of flesh samples in 1973 and 1974 for a study on mercury content.

Another activity which is standard procedure, but less visible, is the monitoring of the radio roundups thrice daily. The data from the roundups are used in an analysis of strikes, catch, and effort in the various areas. Several months after the tournament when all the data analyses have been completed, a report of the results of the activities of NMFS is distributed to the contestants.

Last year, a small portable computer was set up at the communications center of the tournament. As each team reported at roundup time, the date were entered into the computer. Within a minute after the last team reported, we had a printout of the strike rate for each area. Phil Parker who was in charge of radio reporting was thus able to relay information on the best areas of the day at the conclusion of each radio roundup.

Science is not the only purpose of the participation of NMFS in HIBT. Another purpose is to provide an educational experience for those who wish it, not only for those participating in the tournament but for the community at large, as well. Towards that end, NMFS has organized and presented workshops, exhibits, demonstrations, and field trips on a research ship. On a less formal basis, the representatives from the Honolulu Laboratory assigned to the tournament may be approached at any time by anyone who has questions related to billfishes. They also supply notes of interesting biological information to the announcer at the weigh-in show.

Perhaps, the most significant and certainly the most far-reaching activity sponsored by NMFS in connection with HIBT was the International Billfish Symposium of 1972. The symposium was the first ever on billfishes and was attended by People from 10 states and 8 countries. Many of them were the world's leading experts in billfishes. The symposium resulted in the publication of 46 scientific papers on billfishes.

The workshops have been on a smaller scale intime and in amount of participation than the symposium. They have, nonetheless, been useful and informative. A diversity of subjects have been covered at the workshops: the biology of blue marlin, mercury content in marlins, the distribution of marlins as related to the current pattern in Kona waters, lures, baits, the Fishery Conservation and Management Act of 1976, billfish migrations, tagging of marlins, and tracking of marlins. The workshops have been open to the public. The Honolulu Laboratory has been responsible in seeing that the workshops are led by experts on whatever subject matter is being presented.

So much for tournament activities. For the rest of this article, I shall review the NMFS research projects concerning billfishes in the Pacific Ocean.

The most important effort on billfishes currently is the locating and accumulating of data in preparation for a billfish stock assessment workshop to be held at the Honolulu Laboratory in early December. A knowledge of the status of the stocks is essential for rational decisions on conservation measures. The leading billfish fishing countries will be represented at the workshop. Scientists from Japan, Republic of China, Republic of China, Republic of Korea, and the United States will pool their data to arrive at estimates of the magnitude of the billfish stocks. Needed for this study are data on catch and effort, areas of catch, individual sizes of billfishes caught, and dates of capture. Commercial fishing data, which make up the bulk of the extant data, are readily available. Data from recreational fishing activities, however, are more difficult to obtain because of the lack of an organized system to record these data. Efforts are now going on to contact allsport fishing clubs in the Pacific in the hope that hidden in their records are treasures of data. Another source of data on recreational fishing is fishing tournaments.

The short-term movements of marlins and how these movements are related to environmental features is the subject of another study. The blue marlin is the species we are presently concentrating on. Movements are determined by attaching a transmitter to a fish and following it with a boat equipped with receiving equipment. The first tract of a blue marlin was made in 1971 withour research ship, the charles H. 1971 with our research ship the Charles H. Gilbert. Subsequent tracks were too short to provide information on blue marlin, but did provide hints on how to improve our tracking performance. Since then, the ship has been sold and I have decided to use smaller boats for tracking. The bulky tracking equipment is now being purchased so that we shall be able to resume the project shortly.

Long-term movements of marlins are being studied by James Squire of the La Jolla Laboratory, which is also part of the Southwest Fisheries Center. Fish are tagged with a vinyl tag and released with the expectation that some of them will be recaptured, hopefully, at some location along the migration route other than the site of release. He depends entirely on sports fishermen to do the tagging. Recoveries are made by sports and commerical fishermen. Most of the tagged fish have been striped marlin (about 10,000) and sailfish (about 5,000) caught off California and Mexico. The tagging of black marlin off Australia has accelerated in recent years and about 700 have been tagged. The tagging of blue marlin lags behind the other species. About 300 have been tagged.

James Squire is also responsible for the annual Billfish Angling Survey which is conducted by the La Jolla Laboratory with the assistance of the International Game Fish Association. Measures of fishing effort and catch by species are obtained in this survey.

To avoid future shortcomings in data from the recreational segment of the fishery, the Honolulu Laboratory is working together with the Hawaii State Division of Fish and Game on a data collecting system. Although the system will be designed for the State of Hawaii primarily, it is our intention that it will be flexible enough to include all the sport fishing areas in the Pacific. The data will be used for periodic updating of the status of billfish stocks.

An important study on the economic and social impact of recreational fishing for large game fishes on the Kona community is almost completed. This study was contracted out to Research Associates, a firm of professional survey specialists.

Walter Matsumoto of the Honolulu Laboratory is conducting an experiment designed to find out whether or not floating platforms anchored at sea will aggregate enough fish for commercial fishing purposes. Although the experiment is commercially oriented, it will have an effect on recreational fishing. Sports fishemen *are, in fact, fishing around the platforms.*

A problem that was serious only in the Kona area, but seems to be spreading throughout the State of Hawaii, is the taking of fish by porpoises. Why this is considered a problem is that the fish are on fishermen's lines, as bait on trolling lines or longlines, or as the catch on bottom fishermen's handlines. We did a preliminary study to define the problem and submitted a research proposal. The proposal has not been approved as yet.

I frequently attend and present talks at meetings of various sport fishing clubs. This activity does not have any specific scientific purpose, but does serve the general purpose of facilitating communication. Through this activity, I have become more aware of what the game of sport fishing is about and the fishermen have become more aware of what fishery science is about.

Fishery research is an interesting, exciting, and challenging occupation. I view it to be as much of a game as the big game that you as big game fishermen play. In my contacts with you, I have come away with the impression that a number of you are interested in getting involved in research projects, that you want to expand your game by participating in my game. Accordingly, inplanning my projects I have included space for your participation If you have a boat and would like to track marlin or yellowfin tuna, if you would like to tag and release marlins, if you would like to keep records in a way that they can be used by science, I invite you to play at my work. I may be contacted at the following address and telephone:

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